EFFECTS OF DEER BROWSE ON WOODY VEGETATION IN FORESTS AT CORALVILLE LAKE, IOWA: FINAL REPORT – 1998 TO 2002

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By:
Dr. Thomas Rosburg
Department of Biology
Drake University
Des Moines, Iowa 50311

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INTRODUCTION

In many urban areas in Iowa and the Midwest, natural resource managers have become increasingly concerned with the ecological effects of deer overpopulation. The high levels of herbivory concomitant with deer overpopulation have two important potential effects on the forest community. One is the direct influence on forest plant species due to selective herbivory. Many species that are sensitive to grazing or browsing could decrease or even disappear, while a few species that are tolerant may increase and become unnaturally dominant. There is anecdotal evidence that in some cases these sensitive species are plants that are high-quality forest species; therefore their loss represents a serious impact on the integrity of forest communities. A second more indirect influence is the potential negative effect that overgrazing and over browsing may have on other forest animals, particularly songbirds, via changes in the structure of the forest vegetation and the availability of nesting sites.

In the late 1990s, an urban deer task force was formed in Polk County, Iowa from several government agencies, natural resources organizations, and civic groups. Their purpose was to evaluate and address the natural and cultural problems associated with deer overpopulation. A recent deer survey completed by the task force indicated that some areas of Polk County have deer populations in excess of 170 individuals per square mile, and many have populations in the range of 50 to 60 individuals per square mile. Wildlife managers consider a sustainable deer population density to be in the range of 8 to 15 deer per square mile.

Similar levels of deer overpopulation were observed in Johnson County during aerial deer surveys conducted at Coralville Lake by the Army Corps of Engineers (Fig. 1). Counts have been done for seven areas surrounding the reservoir from 1999 to 2003. Three of the study sites in this study occur on the eastern side of tract 2. The fourth study site is located in the southwest section of tract 7. Tract 1 lies between tracts 2 and 7 and is adjacent to all four study sites. In 1999, the second year of this study, deer densities appeared to be close to sustainable levels for most areas, especially the study site areas. Since then however, deer population density in the study site areas has ranged from 2 to 5.5 times greater than the sustainable population size. Growing awareness and concern about the negative effects of high deer herbivory on forest communities and their biodiversity has elevated the deer

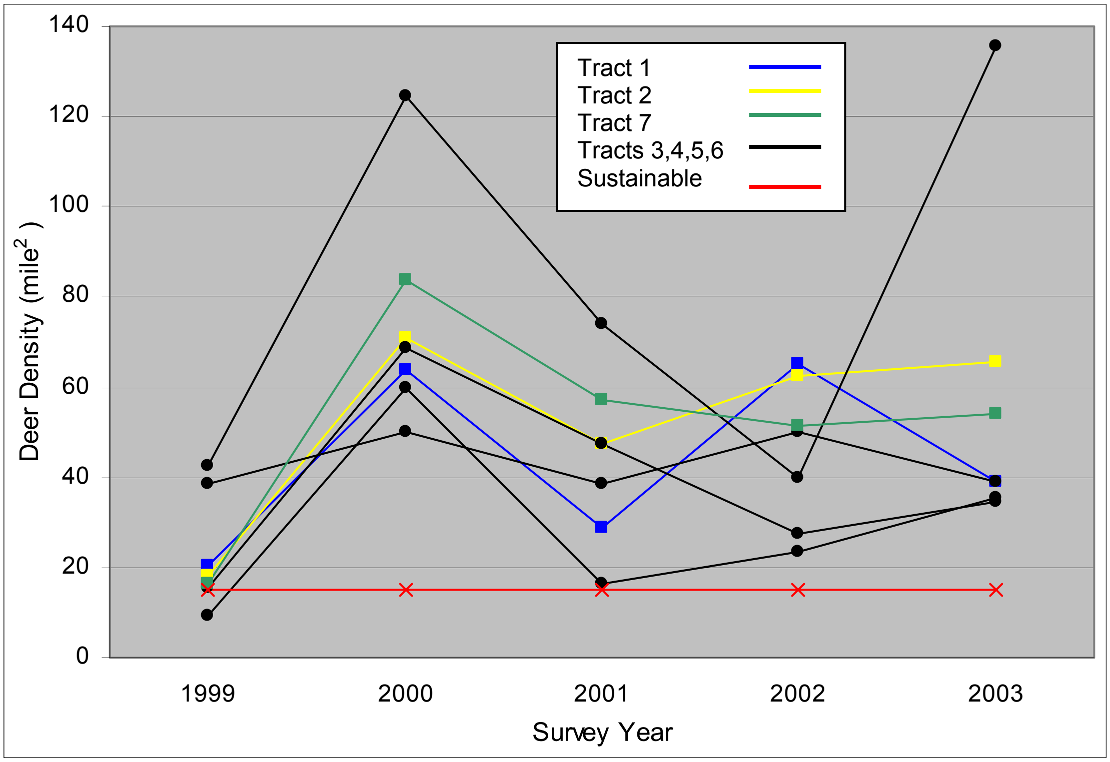

Fig. 1. Deer densities at Coralville from 1999 to 2003 based on winter aerial surveys. Tract 2 encompasses the Linder and West Overlook sites. Tract 7 includes Turkey Creek. Tract 1 is adjacent to all the study sites. Unpublished data from Army Corps of Engineers.

overpopulation issue to prominence. Research is needed to gain a better understanding of the impact deer have on Midwestern forest communities.

The principle objective of this research was to assess the effects of deer herbivory on forest vegetation at Coralville Lake in Johnson County near Iowa City. The approach was to monitor the community composition of woody plant species in study plots inside and outside of deer exclosures. Assuming that at least moderate levels of deer herbivory currently occur at the study sites, then over time the vegetation inside the deer exclosures should exemplify the growth and species composition that results from the release of deer herbivory. These changes will be isolated from the effects of other factors like climate, small herbivores, and pathogens by comparing changes inside the exclosure with the changes that occur in browse plots (control plots for the effect of release from herbivory). An important assumption is that moderate to intense levels of deer herbivory have occurred at all the study sites at Coralville during the duration of the study.

METHODS

Study Sites and Plot Design

Study sites were established by U. S. Army Corps personnel at four locations at Coralville Reservoir during the summer and fall of 1997 (Fig. 2). The West Overlook site occurs on a gentle west-facing slope associated with a broad ridge top. The Linder East and Linder West sites are in an upland area on a gentle north-northeast slope. West Overlook and Linder plots occur in tract 2 of the deer survey. The Turkey Creek site is on the lower north-facing slope of a narrow valley below the dam and lies in tract 7 of the deer survey.

Figure 2. Color infrared aerial 2002 photograph of the dam area at Coralville Reservoir, showing the locations of the deer herbivory study sites.

At each study site two plots approximately 15 x 15 meters were established – one that coincided with the fence of a deer exclosure and one located outside and adjacent to the exclosure. The exclosures were constructed with woven wire fencing and are approximately 2.5 m (8 feet) tall. Gates were built in a corner of the exclosure to permit access. The browse plots outside the exclosure are delineated with a single steel post in each of the four corners.

The study plots are also used for deer browse studies conducted by Steve Hendrix from the University of Iowa at Iowa City. For his study of the effect of deer browse on vegetation structure, 16 sample points were established in a 4 x 4 grid within each plot and marked with short iron rods. Each of the four north-south rows of grid points were used to establish the centerlines of four belt transects utilized in this study (Fig. 3). Each belt transect was 1 meter wide and 12 meters long. Vegetation samples were measured in six 1-m^2 quadrats within each belt transect, one centered within each 2 meter interval of the transect, for a total of 24 1-m^2 quadrats in the entire plot (Fig. 3).

<u>Field Methods</u>

Only woody plants, including liana species, were measured in this study. Herbaceous species were not monitored; however, herbaceous data were collected in the plots by Hendrix (2000, 2001). Effects of deer herbivory on herbaceous plant species were also assessed in another deer herbivory study completed in central Iowa (Rosburg 2002).

Woody vegetation was separated into three structural layers by size classes. Seedling-sprouts are the smallest class and are defined as woody stems less than 50 cm in height. Shrubs comprise the next larger size class and are defined as woody stems between

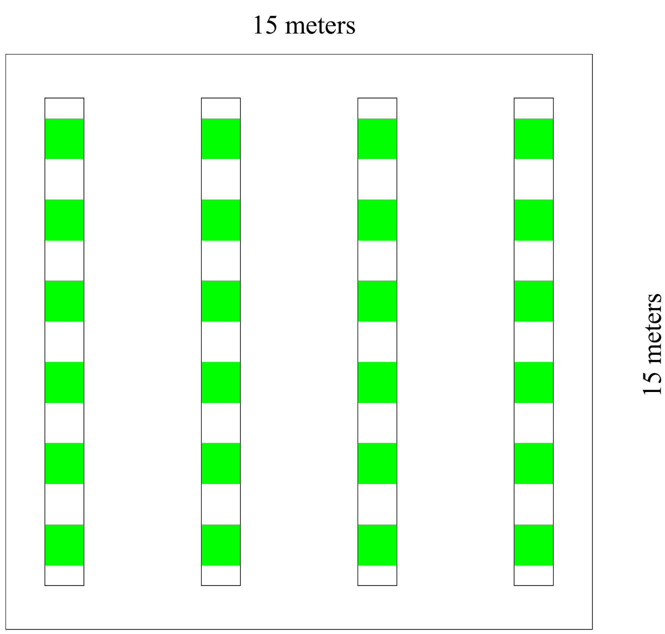

Fig. 3. Plot design at the Coralville study sites. Plots were approximately 15 x 15 m and contained 4 belt transects 1 x 12 m. The shaded areas within the belt transects are 1 x 1 m^2 quadrats where seedling-sprout and shrub species were inventoried.

50 and 200 cm in height. The stem density of both the seedling-sprouts and the shrubs were recorded in the 1-m^2 quadrats. The stem density of saplings, which were defined as woody stems greater than 200 cm in height and less than 5 cm diameter at breast height (DBH), was measured within the entire 15 x 15 m plot.

All plant species that can become woody were inventoried, and many of these have the potential to be present in two or three of the size classes. In general the measurement of stem densities was straightforward and objective. For a few species however, special consideration was necessary. The abundance Virginia creeper (*Parthenocissus* spp.) was only measured when stems were present in the shrub or sapling classes. This species either vines upward on tree trunks or vines along the ground surface. When on the ground, its stem density is nearly impossible to determine, thus Virginia creeper in the seedling-sprout class was not measured. For a few species, the presence of low branching from the primary stem made identification of stems more subjective. If the "branches" arose from the base of the plant near the caudex they were counted as stems from a multiple-stemmed individual. This occurred most often with individuals of bittersweet (*Celastrus scandens*) and gooseberry (*Ribes* spp.).

Plot inventories were initiated in June 1998, the first growing season after construction of the exclosures. Inventories were completed twice during the growing season – once early in the growing season (May or June) and once at the end of the growing season (September) – in 1998, 1999, and 2001. The seventh and last inventory was conducted in May 2002. Spring and fall inventories were conducted to distinguish browsing effects caused by herbivory during the growing season from those caused by herbivory during the dormant season. Species nomenclature follows Eilers and Roosa (1994). In several cases positive identification to the species level was not possible because of the immaturity of individuals in the structural layers inventoried. In these cases identification was to genus. Also, sugar maple (*Acer saccharum*) and black maple (*A. nigrum*) were not distinguished due to their strong similarity; rather they are identified as the species hard maple (*Acer nigrum*). Many taxonomists consider them to be the same species. Table 1 lists all taxa observed in the study and provides names of likely species for plants identified at the genus level. It also cross references scientific names with common names.

Table 1. Woody taxa observed in the Coralville plots arranged by growth form. Origin (O) is either native (N) or exotic (E). Probable species are given for the generic taxa.

O	Scientific Name	Common Name	O	Scientific Name	Common Name
	SHRUBS			LIANAS	
N	*Rhus glabra*	smooth sumac	N,E	*Celastrus* sp.	bittersweet
N	*Ribes* sp.	gooseberry		*scandens, orbiculatus*	
	missouriense, cynobasti		N	*Parthenocissus* sp.	Virginia creeper
N	*Rubus allegheniensis*	blackberry		*quinquefolia, vitacea*	
N	*Rubus occidentalis*	black raspberry	N	*Smilax hispida*	green briar
N	*Symphoricarpos sp.*	buckbrush	N	*Vitis riparia*	wild grape
	orbiculatus, occidentalis		N	*Toxicodendron radicans*	poison ivy
E	*Berberis* sp.	barberry			
	thunbergii, vulgaris			CANOPY TREES	
E	*Elaeagnus* sp.	autumn olive	N	*Acer negundo*	boxelder
	angustifolia, umbellata		N	*Acer nigrum*	hard maple
E	*Lonicera* sp.	honeysuckle	N	*Carya cordiformis*	bitternut hickory
	maackii, tartarica		N	*Carya ovata*	shagbark hickory
E	*Rosa multiflora*	multiflora rose	N	*Celtis occidentalis*	hackberry
E	*Viburnum* sp.	viburnum	N	*Fraxinus* sp.	ash
	opulus			*pennsylvanicum*	
			N	*Gleditsia triacanthos*	honey locust
			N	*Juglans nigra*	black walnut
	UNDERSTORY TREES		N	*Juniperus virginiana*	eastern red cedar
N	*Cornus alternifolia*	alternate leaf dogwood	N	*Prunus serotina*	black cherry
N	*Cornus* sp.	dogwood	N	*Quercus alba*	white oak
	drummondii, foemina		N	*Quercus borealis*	red oak
N	*Corylus americana*	hazelnut	N	*Tilia americana*	basswood
N	*Ostrya virginiana*	ironwood	N	*Ulmus* sp.	elm
N	*Prunus virginiana*	choke cherry		*rubra, americana*	
N	*Zanthoxylum americanum*	prickly ash	E	*Morus alba*	white mulberry
E	*Rhamnus cathartica*	buckthorn			

Analytical Methods

The abundance of species within each of the three structural layers – seedling-sprout, shrub, and sapling classes – was assessed with density (number of stems per unit area). Frequency measurements were also obtained (percentage of presence in 24 1-m^2 quadrats) for the seedling-sprouts and shrubs, but they do not provide the same level of precision as density. Therefore density measurements were used to characterize differences in the species composition of the study plots. The percentage of sapling stems that were dead was also calculated.

The inventory data provide information that can be assigned to one of three general types. The first is basic descriptive information on the community composition of the four study sites from 1998 to 2002. For example, which species are the most common in the different size classes? How abundant are exotic species? The second type of information provides community comparisons between the browse and exclosure plots. Numerous community variables were assessed to determine the effects deer herbivory has on forest structure and composition. The third type of information compares population data (density measurements) of specific species that were present on the study sites to ascertain effects of herbivory (i.e., differences population growth between the browse and exclosure plots).

The experimental design incorporates pairing in both space and time. Measurements on the same plot from any two sample dates are repeated measurements and are therefore paired. Likewise, measurements from the plots at the same site on the same date are spatially paired since the sites represent spatial blocks. Therefore analytical comparisons between the browse and exclosure plots were made with repeated measurement techniques (e.g., paired t-tests). This analytical approach helps to reduce sampling error by using the variance of the differences between the paired observations rather than the variance of the observations. In this way, variation due to different study site environments is minimized. Tests for normality were completed to verify conformity to parametric conditions. If date were not normal, the signed rank test was used and medians were reported. The four sites were used as replicates for all univariate analyses.

The repeated sampling dates are an essential component of the study design. Obviously the effects of environmental variables on vegetation accrue over time. The release from herbivory imposes a new environment on the forest vegetation and although it is possible that some effects could be manifest immediately, most will likely require some time. Data analysis after the first two years of the study indicated that some differences were discernible. A significant browse effect was observed in the percentage of exotic species richness (the percent of exotic species present out of the total number of species). Average exotic species richness increased from 11.4% to 13.4% in the browse plots between June 1998 and September 1999, but decreased from 23.9% to 12.6% in the exclosure plots over the same time period. Thus deer browsing favored the establishment and occurrence of exotic species (Rosburg 2000).

A significant browse effect was also observed in the number of species either increasing or decreasing in density between June 1998 and September 1999 (Rosburg 2000). Browsing reduced the average number of species that increased in density in the shrub and sapling classes. Browsing also increased the average number of species decreasing in the shrub class. Thus browsing was shown to be detrimental to more species (reducing densities) than it is beneficial. This would be expected to decrease biodiversity by decreasing community evenness.

This report has the benefit of 2½ more years and 3 more sample dates for a total of 7 sampling dates over 4½ years. Analysis of the repeated sampling dates was incorporated into the comparisons between browse and exclosure plots in different ways, depending on the variables. For the community variables describing the structure and composition of the forests, the approach used was one that summarized the observations over time in terms of a trend, and then compared the trend between the browse and exclosure plots. Linear regression was used to describe the linear trend in the data over the 4½ years of sampling dates. Since the exclosures were completed in November 1997, that was considered the date at which browsing effects could have initiated. Sampling date was converted to a time variable (months since November 1997) and used as the independent variable in the regression. Regression specifically determined for each plot whether a significant increase or decrease in the variable occurred over time (i.e., linear slope significantly different from 0). The slopes from the paired browse and exclosure plots were then analyzed as a univariate variable with paired t-tests.

One advantage of this approach is that herbivory effects can be recognized at different scales. The best evidence of herbivory effects is those that are demonstrated at all of the sites (i.e., over all of the replicates). Such results show strong uniformity of effects despite differences in environment and history that are inherent in the different sites. However, variation in the level of herbivory during the study period can be problematic in that not all sites may experience the same amount or type of deer herbivory (i.e., differences in treatment intensity or application) and therefore would not be expected to respond in similar ways. Thus it is important to evaluate herbivory effects within sites as well as among sites. In this analysis, within site effects can be recognized by different slopes in the browse and exclosure plots. If the same difference in slopes is consistent among all sites, then even stronger evidence of herbivory effects is demonstrated.

The quantitative community variables included in this analysis are:

1 – total density of all native species (stems/m^2); observed for all three structural layers (seedling-sprouts, shrubs, and saplings).

2 – total density of all exotic species (stems/m^2); observed for all three structural layers.

3 – total density of all species (stems/m^2); observed for all three structural layers.

4 – relative density of native species (%), or the percentage of total density comprised by native species; observed for all three structural layers.

5 – seedling-sprout to shrub ratio, an index reflecting the total density of all seedling-sprouts to the total density of all shrubs (native and exotic). One of the potential effects of deer herbivory is reduction of the height of woody stems from shrub size to seedling-sprout size. An increase in the number of individuals in the seedling-sprout class with a simultaneous decrease in the number of individuals in the shrub class can best be detected with the seedling-sprout/shrub ratio. An increasing ratio indicates stems added to the seedling-sprout class and/or stems lost from the shrub class.

6 – native species richness (number of native species); observed for all three structural layers.

7 – exotic species richness (number of exotic species); observed for all three structural layers.

8 – species richness quality index, calculated as (native richness + 1)/(exotic richness +1); an increasing index reflects greater quality in terms of native and exotic species; observed for all three structural layers; (addition of 1 needed to avoid division by 0). Slight increases in the number of native species or decreases the number of exotic species may not be detectable against background variation. If both occur, their detection is more likely with the species richness quality index because it emphasizes their proportional change. The species richness quality index is more useful than a simple percentage of native species because it integrates species richness as well as proportional differences. For example two communities, one with 4 native and 2 exotic species and one with 20 native and 10 exotic species, have an equal percentage calculation since both have 67% of their species native. However, using the species richness index, the first one has a lower quality index (1.7) due to its overall lower richness than the second (1.9), although both are relatively low due to a high proportion of exotic species.

A multivariate approach was also utilized to assess community effects due to herbivory. An ordination was performed with the plot inventories using DECORANA. The structural information in the inventories was retained in the ordination by using the concept of pseudospecies. Species that were present in more than one structural layer were recorded as if "separate species." For example, dogwood (*Cornus* spp.) was present in all three structural layers, thus there were three dogwood pseudospecies – dogwood seedling-sprout, dogwood shrub, and dogwood sapling – each treated as a distinct species. In this way structural variation among the plots contributed to plot differences just as much as variation in species composition. The goal of an ordination is to summarize large amounts of complex data. The community composition of each sample (i.e., in this study each plot and sample date combination) is represented as a single point and located in a two dimensional space that encompasses the total variation in species composition among all the community samples. The amount of similarity/dissimilarity in species composition among the community samples is reflected by the distance between samples in the ordination. Samples close to one another are similar in species composition; samples distant from one another are dissimilar in species composition.

Three sapling pseudospecies were excluded from the ordination due to their liana growth habit. Much of the bittersweet recorded in the exclosure plots were lianas vining on the exclosure fence. Thus the abundance of bittersweet was greatly affected by the presence of the wire fence to make the exclosure, and not necessarily the release from grazing. The exclosure fence made an ideal substrate for vining, which provided better accessibility to light and likely enhanced its growth and vegetative reproduction. Similar effects of the wire fence on the growth of the lianas Virginia creeper and poison ivy are expected. In addition, Virginia creeper and poison ivy lianas were difficult to distinguish because the canopies of the trees on which they were vining tended to obscure their leaves. Therefore sapling pseudospecies of bittersweet, Virginia creeper and poison ivy were excluded from the species composition data used in the ordination.

The third type of information reported, the quantitative comparison of herbivory effects on species' population densities, assessed the change in density of a species during a specific period, using an earlier inventory as a baseline and a later inventory as the response. The amount of potential change in absolute density, either up or down, depends on the baseline density. In order to assess the change independent of variation among plots in the baseline density, population per capita growth rates were calculated for each period. This term (r) expresses the amount of change in density during the period as the number of stems increasing or decreasing per stem in the baseline population.

$$r = \left(\frac{\ln\left(\frac{N_t + 0.01}{N_0 + 0.01}\right)}{t} \right)$$

where:

N_0 = baseline density at time 0

N_t = density at time t

t = length of the period in years (therefore this is an annual per capita growth rate)

Use of per capita growth rates allows assessment of herbivory effects between any two sampling dates and utilizes the starting density as a control of natural variation. It was necessary to add a nominal density (0.01) to each sampled density to avoid a denominator of 0. Per capita growth rates were calculated for each time period between sample dates and for the entire study period from beginning to end. Per capita growth rates (number of stems added or lost per stem in the population) characterize the change in stem density between sample dates for both the browse and exclosure plots, and were compared with paired t-tests using replication provided by the sites.

It is likely that deer herbivory was heterogeneous throughout the study period with high and low intensities at different times. By analyzing each period between sample dates, effects of herbivory on certain species may be discovered that would not be apparent with a single analysis over the entire period. In addition, this approach also allowed a comparison of herbivory effects during the growing season (May to September) with those occurring during the dormant season (September to May).

The species included in this analysis were the more common seedling-sprout and shrub species, specifically those that were present on at least three of the sampling dates and at three or four of the sites (in order to have acceptable replication). In some cases, when species of interest were not present at enough sites or dates, species in the same genus were grouped together to obtain better representation and replication (e.g., *Quercus*, *Rubus*).

RESULTS AND DISCUSSION

General Description of Woody Communities at Coralville

The seven species inventories completed between 1998 and 2002 recorded a total of 37 woody taxa. Among these, 15 are overstory tree species, 7 are understory species, 10 are shrub species, and 5 are lianas (Table 1). Among the 37 taxa, 7 are exotic species (5 shrubs, 1 understory tree, and 1 canopy tree). The general abundance of these species, regardless of plot type or time of sample, provides basic information about the woody composition of the forest communities at Coralville. The overall mean densities were determined for all the taxa observed in each of the three structural layers (Table 2). Bittersweet (*Celastrus* sp.) was by far the most common species observed; it was the most abundant species in each of the three layers (Table 2). Its mean density in the seedling-sprout class (about 3.5 stems/m^2) and shrub class (1.2 stems/m^2) was 2 to 2.9 times as dense as the next most common species in the seedling-spout layer, black cherry (*Prunus serotina*, 1.2 stems/m^2) and the next most common species in the shrub layer, gooseberry (*Ribes* spp., 0.6 stems/m^2). Both bittersweet and dogwood (*Cornus* spp.) were more than 3 times as dense as the next most common species in the sapling class (Table 2). It is certain that the vast majority of bittersweet was the native species *Celastrus scandens*. However, Coralville personnel have tentatively identified some specimens of the exotic oriental bittersweet (*Celastrus orbiculatus*), thus it is possible that a small amount of it is also represented in the bittersweet data. Other very common native species included black cherry, gooseberry, dogwood, elm (*Ulmus* spp.), poison ivy (*Toxicodendron radicans*), ash (*Fraxinus* sp.), hard maple (*Acer nigrum*) and bitternut hickory (*Carya cordiformes*) (Table 2). Six of the seven exotic species placed in the top 15 species of at least one of the three size classes. Multiflora rose *(Rosa multiflora)*, autumn olive (*Elaeagnus* spp.), and white mulberry (*Morus alba*) were the most abundant exotic species.

Table 2. Mean densities of woody species observed in plots at Coralville. Means are based on 56 samples (all 8 plots sampled over all 7 dates). Density is presented in stems per decihectare (10 x 10 m area). Species with an (*) are non-native.

Seedling-Sprouts	Mean Density (st/dha)	Shrubs	Mean Density (st/dha)	Saplings	Mean Density (st/dha)
Celastrus sp.	354.5	Celastrus sp.	117.8	Celastrus sp.	8.42
Prunus serotina	120.4	Ribes sp.	57.4	Cornus (racemosa)	7.89
Ribes sp.	105.3	Prunus serotina	21.9	Prunus serotina	2.29
Toxicodendron radicans	52.5	*Rosa multiflora	17.7	Fraxinus sp.	1.39
Ulmus sp.	50.1	*Elaeagnus sp.	15.5	Acer nigrum	1.23
*Rosa multiflora	46.3	Cornus (racemosa)	12.9	Parthenocissus sp.	1.10
Vitis riparia	25.2	Rubus allegheniensis	6.6	Carya cordiformis	1.03
Smilax hispida	20.2	Carya cordiformis	4.5	Acer negundo	0.97
Fraxinus sp.	17.9	Rubus occidentalis	4.5	Corylus americana	0.89
Cornus (racemosa)	16.9	Acer negundo	3.5	*Elaeagnus sp.	0.41
Carya cordiformis	16.7	*Viburnum sp.	2.3	Toxicodendron radicans	0.27
*Elaeagnus sp.	16.2	*Lonicera sp.	1.7	Ulmus sp.	0.21
Rubus allegheniensis	9.2	Fraxinus sp.	1.6	*Morus alba	0.18
*Rhamnus cathartica	7.9	Ulmus sp.	1.6	Carya ovata	0.18
*Viburnum sp.	6.8	Acer nigrum	1.3	Ostrya virginiana	0.15
Gleditsia triacanthos	6.3	Vitis riparia	1.3	Rhus glabra	0.13
*Morus alba	5.3	Carya ovata	1.2	Vitis riparia	0.11
Quercus borealis	5.0	*Berberis sp.	1.0	Cornus alternifolia	0.09
Celtis occidentalis	4.8	Corylus americana	0.8	*Rosa multiflora	0.08
Acer nigrum	4.5	Toxicodendron radicans	0.8	Quercus borealis	0.08
Rubus occidentalis	4.5	*Morus alba	0.7	Celtis occidentalis	0.08
*Berberis sp.	4.1	Parthenocissus sp.	0.7	Ribes sp.	0.06
Acer negundo	3.9	Rhus glabra	0.6	Juglans nigra	0.06
Ostrya virginiana	3.1	Celtis occidentalis	0.4	Quercus alba	0.05
Carya ovata	2.3	Ostrya virginiana	0.4	Rubus occidentalis	0.04
*Lonicera sp.	2.0	Quercus alba	0.4	Tilia americana	0.03
Juniperus virginiana	1.8	Smilax hispida	0.3	Rubus allegheniensis	0.02
Quercus alba	0.7	*Rhamnus cathartica	0.1	Prunus virginiana	0.004
Rhus glabra	0.7	Cornus alternifolia	0.1		
Cornus alternifolia	0.5	Quercus borealis	0.1		
Tilia americana	0.3	Tilia americana	0.1		
Symphoricarpos sp.	0.2	Zanthoxylum americanum	0.1		
Corylus americana	0.1				
Juglans nigra	0.1				
Zanthoxylum americanum	0.1				

There was considerable variation in the total densities of woody vegetation among the four sites. Total seedling-sprout densities ranged from about 2 stems/m^2 at Turkey Creek to 16-17 stems/m^2 at West Overlook and Linder West. Shrubs were the least variable size class, with a range of total density from 0.5 stem/m^2 at Turkey Creek to 5-6 stems/m^2 at West Overlook. Total sapling density was extremely variable, ranging from about 500 stems/ha at Turkey Creek to nearly 8,000 stems/ha at West Overlook. Native species richness was highest in the seedling-sprout class, and ranged from 5 at Turkey Creek to 18-19 at Linder West and West Overlook sites. Shrub native richness ranged from 1 at Turkey Creek to 12 at Linder East and West Overlook, while sapling native richness ranged from 4 at Turkey Creek to 10-12 at all three other sites. Exotic species were most numerous at West Overlook (4-7 seedling-sprouts, 2-6 shrubs, and 1-3 saplings), intermediate at Linder East and Linder West (1-6 seedling-sprouts, 0-3 shrubs, and 0-2 saplings), and absent from Turkey Creek.

Overall, woody vegetation was the densest at West Overlook. Linder West was comparable to West Overlook in terms of seedling-sprout and shrub density, but it has much lower sapling density (about 35% of West Overlook). Linder East has similar woody structure as Linder West except that the seedling-sprout density for Linder East is about 55% of the density at Linder West. Woody vegetation is the sparsest at Turkey Creek, with seedling-sprout density about 35% of the seedling/sprout density at West Overlook, about 25% of the shrub density at West Overlook, and sapling density less than 10% of sapling density at West Overlook.

Among the seedling–sprouts, 35 of 36 species (Virginia creeper was excluded from this size class) were observed; only chokecherry (*Prunus virginiana*) was not observed in the seedling-sprout stage. In the shrub class, 32 of the 37 species (86%) were present in the plots. Species missing from the shrub layer included mostly trees (honey locust, black walnut, eastern red cedar, chokecherry) and one shrub (buckbrush). There were 28 of the 37 species (76%) present in sapling layer. Missing species included shrubs not likely to grow large enough to be saplings (barberry and buckbrush), other shrubs (honeysuckle and viburnum), lianas (green briar), and trees (prickly ash, buckthorn, honey locust, eastern red cedar).

General Community Composition Patterns (Ordination)

Variation in woody structure and species composition are depicted graphically in the ordination (Fig. 4). West Overlook and Turkey Creek, which occur at opposite ends of DCA axis one, are the most different compositionally. The more dense and species rich (including exotic species) West Overlook plots are represented with low DCA axis one scores, while the more sparse Turkey Creek plots are represented with high DCA axis one scores. The species composition of the forest community at West Overlook is characterized by shrub and successional forest species such as smooth sumac, autumn olive, eastern red cedar, buckthorn, honeysuckle, prickly ash, and wild grape (Table 3, axis 1 low scores). The forest community at Turkey Creek is a more mature forest as exhibited by the higher abundance of several tree species such as white oak, basswood, ironwood, hard maple and red oak (Table 4, axis 1 high scores). The browse and exclosure plots at West Overlook and Turkey Creek are fairly similar to one another, thus these species are characteristic of both plots at each respective site. In fact, the browse and exclosure plots at both West Overlook and Turkey Creek are more similar to one another (at the site) than they are to browse or exclosure plots elsewhere (Fig. 4).

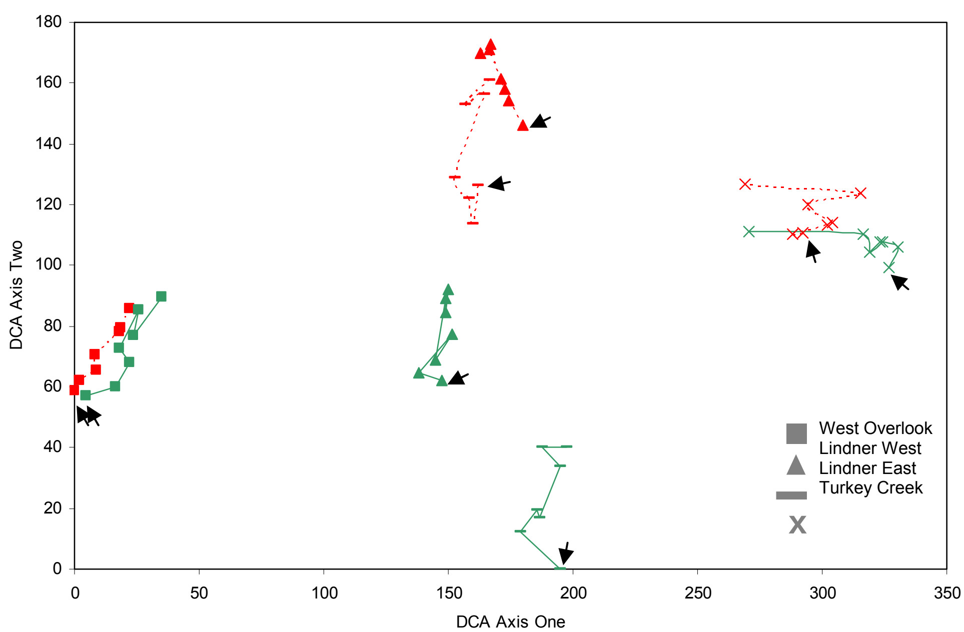

Fig. 4. DECORANA ordination of browse plots (red) and exclosure plots (green) at all Coralville study sites on all seven sample dates. Arrows indicate the first sample date (June 1998); sequential sample dates occur in order along the line connecting the points.

Table 3. Woody pseudospecies characteristic of the ends of DCA axis 1 and 2 (Fig. 3). Presence on segments of the axes is indicated with an "x" for the seedling-sprouts (ss), shrubs (shb), and saplings (sap) size classes.

Common Name	ss	shb	sap	Common Name	ss	shb	sap
	Axis 1 - high				Axis 2 -high		
White oak		x	x	Black walnut	x		
Basswood	x	x	x	Wild grape			x
Ironwood	x	x	x	Hackberry			x
Red oak		x		Hard maple		x	
Hard maple		x	x	Shagbark hickory		x	
Gooseberry	x						
	Axis 1 - low				Axis 2 -low		
Smooth sumac	x	x	x	Hazelnut	x	x	x
Autumn olive	x	x	x	Raspberry, Blackberry			x
Eastern red cedar	x			Alternate leaf dogwood			x
Buckthorn		x		Virginia creeper		x	
Honeysuckle sp.		x		Gooseberry			x
Alternate leaf dogwood	x	x		Hackberry		x	
Prickly ash	x	x		Multiflora rose			x
Dogwood sp.			x	Green briar		x	
Wild grape	x	x		White mulberry			x
Chokecherry			x				
Ash	x	x					
Poison ivy		x					
White mulberry	x						

A different situation is present at the Linder Point sites. The browse plots at Linder East and Linder West are more similar to one another than they are to their companion exclosure plots. The variation in species composition represented along DCA axis two is characterized by the species differences in the Linder East exclosure (low scores on DCA axis two) and both of the Linder browse plots (especially Linder West) which occur on the high end of DCA axis two. Young tree species such as black walnut, hackberry, hard maple and shagbark hickory as well as large wild grape vines characterize the high end of DCA axis two and are distinctive of the Linder browse plots (Table 3). A group of shrub and successional forest species characterize the Linder East exclosure (Table 3, axis 2 low scores) that are different from the successional species at West Overlook. They include hazelnut, blackberry, raspberry, alternate leaf dogwood, Virginia creeper, hackberry, and gooseberry. Not only are the shrub and successional species different at the Linder East exclosure, they are primarily in the shrub and sapling size classes as opposed to a much higher proportion of seedling-sprouts and lower proportion of saplings at West Overlook (Table 3). West Overlook has more diversity of species and size classes, while Linder East exclosure has relatively older individuals in the understory (i.e., in an older stage of woody succession).

The primary source of variation in species composition (seen on DCA axis one, Fig. 4) is clearly the successional status of the forest, from early successional (i.e., more recent disturbance) at West Overlook to late successional at Turkey Creek. The Linder sites are mid-successional along this gradient. The second most important cause of variation in species composition (seen on DCA axis two, Fig. 4) is most manifest in differences between Linder East exclosure and Linder West browse. Although browsing effects are implicated as an environmental factor causing this variation, the bulk of this variation was present at the beginning of the study (in June 1998) and therefore is not associated with browse effects (Fig. 4). Also, changes in species composition associated with environmental changes during the 4½ years of the study (represented by the lines connecting samples from the same site) mostly correspond to DCA axis two (at all sites except Turkey Creek). Thus the variation represented on DCA axis two has multiple sources – herbivory, climate, pathogens, and inherent spatial differences – that have similar effects on species composition.

The initial species composition of the plots in June 1998 (Fig. 4, arrows) accounts for nearly all of the variation observed over the 4½ years of inventories. Exclosure and browse plots at West Overlook and Turkey Creek had fairly similar initial community compositions, which indicate the vegetation is relatively homogenous at each of these sites. In contrast, the initial compositions of the exclosure and browse plots at both Linder East and Linder West were quite different, implying a considerable amount of spatial heterogeneity occurs at the Linder sites. It is this heterogeneity that defines most of the variation contained in DCA axis two.

The ordination does not show a strong effect of browsing on the community composition of the forests. Such an effect would be best demonstrated by browse and exclosure plots that were initially similar, but then diverge over time. The pattern seen at West Overlook and Turkey Creek is certainly not divergence; rather the path of the browse and exclosure plots over time follows a fairly parallel course. The Linder sites exhibit some divergence in the path of browse and exclosure plots over time (indicating some browse effect on community composition). This is best seen at Linder West, where the browse plots tend to move down DCA axis one (becoming more early successional) while the exclosure plots tend to move up DCA axis one (becoming more late successional). Community composition of browse and exclosure plots at Linder East are the most different among all the sites, but nearly all of this dissimilarity was inherent and present at the beginning of the study (also true for Linder West). Although the pathways for the browse and exclosure plots at Linder East are similar in their overall direction, there is a more erratic pattern in the sample to sample trajectories than at West Overlook and Turkey Creek, indicating browse effects for some of the sample dates within the study period.

The prevailing pattern in the ordination is that both the amount and direction of change in community composition of the plots over the course of the study was very similar at all four sites. The only exception to this general result was that the direction of change seen at Turkey Creek was noticeably different from the other three sites. Turkey Creek plots experienced a retrogressive successional change over time (from late successional to mid-successional with main direction towards lower axis one scores), Linder plots moved vertically up axis 2 (increased abundance of canopy tree species in the understory), and West Overlook experienced both a progressive successional change and an increase in canopy tree species in the understory (upward direction on both axes). The browse effects that did occur are relatively small compared to the changes that occurred at all sites over the 4½ years of the study and to the large differences that are inherent in the sites.

The large amount of inherent variation in community composition among the sites suggests that variation in the historic intensity of deer herbivory, or other environmental factors, has been considerable among the sites. Such natural variation in composition adds complexity to the study in various ways. Biotic environments are obviously quite different between Turkey Creek and West Overlook for example, which can influence establishment and growth of woody species. Deer use of the sites, which may have contributed to this heterogeneity, may be quite different because of the current variation in composition and structure. If browse effects are to be discovered, then variation in composition due to the release from deer herbivory must be separated from all other variation, hence the importance of the control (browse) plots and utilization of baseline or initial composition in comparisons.

Hendrix (2001) reported several significant deer herbivory effects on forest vegetation between 1998 and 1999. Specifically herbivory decreased the foliage height diversity, it decreased the evenness of foliage height, and it decreased the number of foliage height intervals present. His study showed deer herbivory effects were foremost evident at Linder East, and second most evident at West Overlook. The expected outcome of deer herbivory was not apparent at two of the sites. In this way, Hendrix (2001) corroborates the pattern observed in the community composition data of this study in that considerable variation in deer herbivory effects occurred among the sites.

Browse Effects on Forest Community Structure

A large amount of the analysis in this study was devoted to comparisons of browse and exclosure plots in regard to numerous forest community structure and diversity variables. These variables are grouped according to the size class of woody vegetation they describe. Linear regression was performed with the data using time (sampling date converted to months after November 1997) as the independent variable. Slopes of paired plots were analyzed with a paired t-test.

Seedling-sprouts

There were no significant browse effects on seedling-sprouts demonstrated uniformly at all four sites (Table 4, paired t-tests all have $p>0.10$). There were however many local effects of browsing demonstrated by the regression analyses. Total density of native seedling-sprouts was increased by browsing on Linder East and decreased by browsing on Turkey Creek (Table 4, Fig. 5). Native seedling-sprouts also increased in density at both West Overlook and Linder West sites, but since the increases occurred equally on both browse and exclosure plots, there was no effect attributable to browsing.

Two sites, West Overlook and Linder West, exhibited an effective decrease in total density of exotic seedling-sprouts due to browsing. In both cases this occurred because significant increases occurred in the exclosure while the browse plots remained unchanged (Table 4, Fig. 6). Total density of exotic seedling-sprouts increased equally in both browse and exclosure plots at Linder East.

The total density of all seedling-sprouts increased due to browsing at Linder East, and decreased due to browsing at Linder West and Turkey Creek (Table 4).

The relative density of native seedling-sprouts is a forest quality assessment that describes the proportion of native abundance of seedling-sprouts irrespective of absolute densities. One site, Linder West, demonstrated an increase in the relative density of native seedling-sprouts due to browsing (Table 4, Fig. 7).

The ratio of total seedling-sprout density to total shrub density provides an index that relates the evenness of these two regeneration stages of woody vegetation. All woody species become at least shrubs at maturity and all woody species pass through both of these classes during regeneration. A large index means there are a lot more seedling-sprouts then shrubs, a condition that could arise by herbivory forcing shrubs into the seedling-sprout class. In this sense the index functions as a measure of browsing intensity. There was a significant increase in the index due to browsing at two sites – Linder East and Turkey Creek (Table 4, Fig. 8).

Native species richness of seeding-sprouts increased due to browsing on Turkey Creek, but effectively decreased due to browsing on West Overlook (Table 4, Fig. 9). Exotic species richness of seedling-sprouts decreased due to browsing on Linder East (Table 4). A measure of forest quality based on the ratio between native and exotic species richness was made to better recognize slight but positive changes in species richness. This index increased due to browsing on Turkey Creek (Table 4).

These results demonstrate the varied outcomes of deer herbivory due to local site environments. The regression analyses for local effects at each site resulted in 14 significant browse effects among all seedling-sprout variables. Each of these effects was assigned either a positive or negative outcome in terms of contribution to forest health and biodiversity (e.g., increasing total native density is positive, Table 5). Altogether there were 8 positive effects (57%) and 6 negative effects (43%) associated with browsing. All four sites experienced both positive and negative effects, although positive browsing effects were more common at the Linder sites and negative browsing effects were more common at Turkey Creek.

Table 4. Seedling-sprout density and species richness from 1998 to 2002 with linear regression and paired t-test results. Sites include West Overlook (WO), Lindner East (LE), Lindner West (LW), and Turkey Creek (TC). P-values less than 0.10 are considered slightly significant, those less than 0.05 are significant.

Variable	Site	Plot	Spring 1998	Fall 1998	Spring 1999	Fall 1999	Spring 2001	Fall 2001	Spring 2002	Reg Slope	P-value	Result Summary and Browse Effects
Total Native Density (Fig. 4)	WO	Br	8.96	11.50	11.08	13.29	12.00	14.67	13.58	0.078	0.043	similar significant increase for both plots; no effect of browse indicated
		Ex	6.71	9.63	11.71	11.17	12.21	10.71	14.13	0.095	0.042	
	LE	Br	4.46	5.29	5.50	8.33	7.21	9.08	8.38	0.080	0.022	significant increase in browse, no change in exclosure; effective increase indicated in browse
		Ex	3.54	4.21	5.67	5.17	4.00	5.79	5.04	0.019	0.37	
	LW	Br	9.13	12.66	13.46	15.46	15.63	14.63	15.83	0.098	0.044	similar significant increase for both plots; no effect of browse indicated
		Ex	7.00	9.50	11.38	11.46	11.67	11.67	13.79	0.095	0.020	
	TC	Br	3.38	3.04	4.17	3.17	5.00	3.21	5.13	0.030	0.13	no change in browse, slight significant increase in exclosure; effective decrease indicated in browse
		Ex	1.92	1.92	2.46	2.92	2.54	2.54	6.83	0.064	0.086	
Mean 2002 Density and Regression Slope for all Browse Plots									10.73	0.064	0.99	overall no significant difference in slopes for browse and exclosure plots; no browse effect
Mean 2002 Density and Regression Slope for all Exclosure Plots									9.95	0.063		
Total Exotic Density (Fig. 5)	WO	Br	0.92	1.17	1.13	1.75	1.33	1.33	1.67	0.0057	0.15	no change in browse, significant increase in exclosure; effective decrease indicated in browse
		Ex	1.21	1.08	1.04	1.33	1.92	2.17	1.71	0.0053	0.013	
	LE	Br	0.38	0.42	1.33	0.79	2.25	2.04	2.75	0.049	0.0005	similar significant increase for both plots; no effect of browse indicated
		Ex	0.21	0.17	1.08	0.54	1.50	1.38	1.67	0.031	0.0028	
	LW	Br	0.33	0.92	0.58	0.96	1.71	0.83	0.58	0.0079	0.46	no change in browse, significant increase in exclosure; effective decrease indicated in browse
		Ex	0.58	0.25	0.54	0.75	1.92	1.29	2.04	0.035	0.0028	
	TC	Br	0.00	0.00	0.00	0.00	0.00	0.00	0.00	no exotic spp.		no test in either plot
		Ex	0.00	0.00	0.00	0.00	0.00	0.00	0.00	no exotic spp.		
	Mean Slope for all Browse Plots								1.25	0.016	0.67	overall no significant difference in slopes for browse and exclosure plots; no browse effect
	Mean Slope for all Exclosure Plots								1.35	0.024		
Total All Density	WO	Br	9.88	12.67	12.21	15.04	13.33	16.00	15.25	0.087	0.045	similar significant increase for both plots; no effect of browse indicated
		Ex	7.91	10.71	12.75	12.50	14.13	12.88	15.83	0.12	0.013	
	LE	Br	4.83	5.71	6.83	9.13	9.46	11.13	11.13	0.13	0.0013	significant increase for both plots, browse increase larger; effective increase indicated in browse
		Ex	3.75	4.38	6.75	5.71	5.50	7.17	6.71	0.050	0.066	
	LW	Br	9.46	13.58	14.04	16.42	17.33	15.46	16.42	0.106	0.056	significant increase for both plots, browse increase smaller; effective decrease indicated in browse
		Ex	7.58	9.75	11.92	12.21	13.58	12.96	15.83	0.13	0.0046	
	TC		3.38	3.04	4.17	3.17	5.00	3.21	5.13	0.030	0.13	no change in browse, slight significant increase in exclosure; effective decrease indicated in browse
			1.92	1.92	2.46	2.92	2.54	2.54	6.83	0.064	0.086	
	Mean Slope for all Browse Plots									0.080	0.78	overall no significant difference in slopes for browse and exclosure plots; no browse effect
	Mean Slope for all Exclosure Plots									0.090		

Table 4

Variable	Site	Plot	Spring 1998	Fall 1998	Spring 1999	Fall 1999	Spring 2001	Fall 2001	Spring 2002	Reg Slope	P-value	Result Summary and Browse Effects
Native Relative Density (%) (Fig. 6)	WO	Br	90.7	90.8	90.8	88.4	90.0	91.7	89.1	-0.010	0.72	no change in either, no effect of browse indicated
		Ex	84.7	89.9	91.8	89.3	86.4	83.2	89.2	-0.042	0.58	
	LE	Br	92.2	92.7	80.5	91.3	76.2	81.6	75.3	-0.34	0.019	similar significant decrease for both plots; no effect of browse indicated
		Ex	94.4	96.2	84.0	90.5	72.7	80.8	75.2	-0.44	0.0066	
	LW	Br	96.5	93.2	95.8	94.2	90.1	94.6	96.4	-0.018	0.74	no change in browse, significant decrease in exclosure; effective increase indicated in browse
		Ex	92.3	97.4	95.5	93.9	85.9	90.0	87.1	-0.19	0.021	
	TC	Br	100.0	100.0	100.0	100.0	100.0	100.0	100.0	no exotic spp.		no test in either plot
		Ex	100.0	100.0	100.0	100.0	100.0	100.0	100.0	no exotic spp.		
	Mean Slope for all Browse Plots									-0.11	0.22	overall no significant difference in slopes for browse and exclosure plots; no browse effect
	Mean Slope for all Exclosure Plots									-0.21		
Total Seedling Sprout Density to Shrub Density (Index) (Fig. 7)	WO	Br	2.9	3.8	3.3	3.6	2.6	2.7	3.5	-0.0079	0.48	no change in either, no effect of browse indicated
		Ex	3.1	4.4	4.0	2.4	2.7	2.1	2.9	-0.027	0.14	
	LE	Br	1.9	2.7	3.2	3.6	4.2	5.0	5.4	0.066	0.0002	significant increase in browse, no change in exclosure; effective increase indicated in browse
		Ex	1.3	1.5	2.0	1.7	1.5	1.8	1.9	0.0061	0.31	
	LW	Br	2.8	4.8	4.7	4.2	5.2	5.4	4.2	0.023	0.24	no change in either, no effect of browse indicated
		Ex	3.1	7.1	4.5	4.3	3.5	3.7	4.0	-0.027	0.39	
	TC	Br	2.3	2.4	5.0	3.3	10.0	5.1	13.7	0.20	0.016	significant increase for both plots, browse increase larger; effective increase indicated in browse
		Ex	1.4	1.4	3.0	3.3	2.1	2.5	8.6	0.088	0.106	
	Mean Slope for all Browse Plots									0.065	0.20	overall no significant difference in slopes for browse and exclosure plots; no browse effect
	Mean Slope for all Exclosure Plots									0.022		
Native Species Richness (Fig. 8)	WO	Br	14	13	16	17	16	16	17	0.056	0.085	significant increase for both plots, browse increase smaller; effective decrease indicated in browse
		Ex	12	14	14	15	16	16	19	0.11	0.0032	
	LE	Br	12	14	14	15	12	14	13	-0.0078	0.78	no change in either, no effect of browse indicated
		Ex	7	15	13	14	12	10	10	-0.028	0.69	
	LW	Br	16	17	16	17	18	15	15	-0.019	0.47	no change in either, no effect of browse indicated
		Ex	10	13	12	15	10	12	13	0.0017	0.97	
	TC	Br	6	7	8	8	12	9	9	0.076	0.055	significant increase in browse, no change in exclosure; effective increase indicated in browse
		Ex	6	5	7	5	5	6	6	0.0004	0.98	
	Mean Slope for all Browse Plots									0.033	0.84	overall no significant difference in slopes for browse and exclosure plots; no browse effect
	Mean Slope for all Exclosure Plots									0.027		

Table 4

Variable	Site	Plot	Spring 1998	Fall 1998	Spring 1999	Fall 1999	Spring 2001	Fall 2001	Spring 2002	Reg Slope	P-value	Result Summary and Browse Effects
Exotic Species Richness	WO	Br	4	4	4	5	4	5	5	0.018	0.14	no change in either, no effect of browse indicated
		Ex	7	5	4	4	6	7	4	-0.0014	0.97	
	LE	Br	1	2	1	2	1	3	3	0.029	0.15	no change in browse, significant increase in exclosure; effective decrease indicated in browse
		Ex	3	2	3	3	3	4	4	0.029	0.032	
	LW	Br	3	4	3	4	4	6	3	0.020	0.45	no change in either, no effect of browse indicated
		Ex	4	2	1	2	3	2	4	0.015	0.58	
	TC	Br	0	0	0	0	0	0	0	no exotic spp.		no test in either plot
		Ex	0	0	0	0	0	0	0	no exotic spp.		
	Mean Slope for all Browse Plots									0.000	0.42	overall no significant difference in slopes for browse and exclosure plots; no browse effect
	Mean Slope for all Exclosure Plots									0.010		
Species Richness Quality: Native S to Exotic S Ratio	WO	Br	3.0	2.8	3.4	3.0	3.4	2.8	3.0	0.0010	0.88	no change in either, no effect of browse indicated
		Ex	1.6	2.5	3.0	3.2	2.4	2.1	4.0	0.019	0.30	
	LE	Br	6.5	5.0	7.5	5.3	6.5	3.8	3.5	-0.048	0.15	no change in either, no effect of browse indicated
		Ex	2.0	5.3	3.5	3.8	3.3	2.2	2.2	-0.030	0.28	
	LW	Br	4.3	3.6	4.3	3.6	3.8	2.3	4.0	-0.015	0.36	no change in either, no effect of browse indicated
		Ex	2.2	4.7	6.5	5.3	2.8	4.3	2.8	-0.024	0.54	
	TC	Br	7.0	8.0	9.0	9.0	13.0	10.0	10.0	0.076	0.055	significant increase in browse, no change in exclosure; effective increase indicated in browse
		Ex	7.0	6.0	8.0	6.0	6.0	7.0	7.0	0.0004	0.98	
	Median Slope for all Browse Plots									0.000	1.00	overall no significant difference in slopes for browse and exclosure plots; no browse effect
	Median Slope for all Exclosure Plots									0.000		

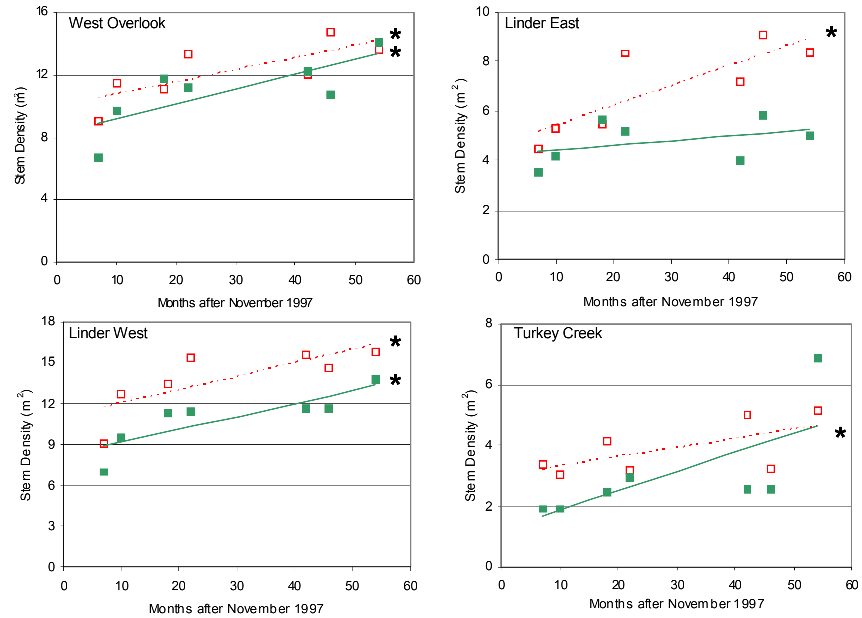

Fig. 5. Total density of native woody seedling-sprout species at Coralville study sites from June 1998 to May 2002. Slopes and p-values for regression lines are given in Table 4. Significant linear regressions ($p<0.10$) are indicated with (*).

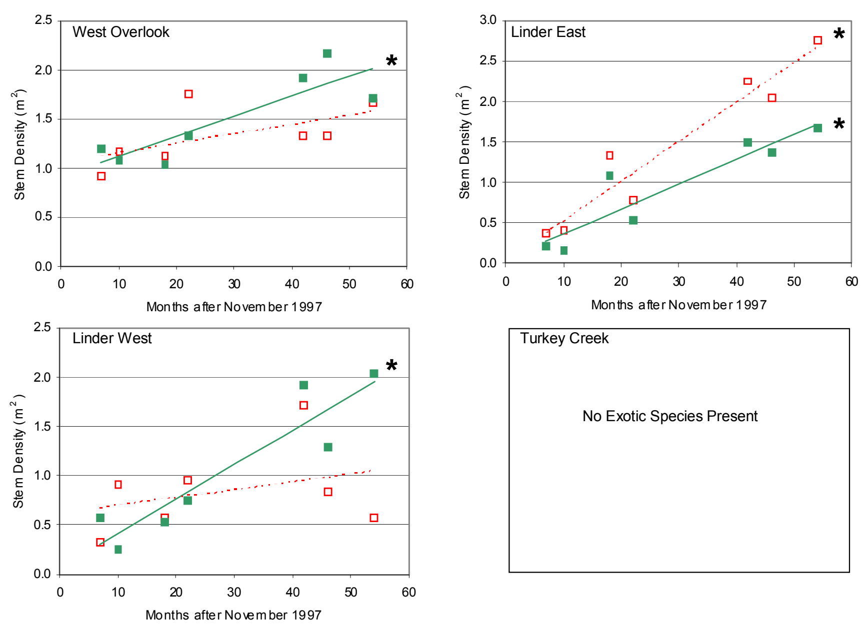

Fig. 6. Total density of exotic woody seedling-sprout species at Coralville study sites from June 1998 to May 2002. Slopes and p-values for regression lines are given in Table 4. Significant linear regressions ($p<0.10$) are indicated with (*).

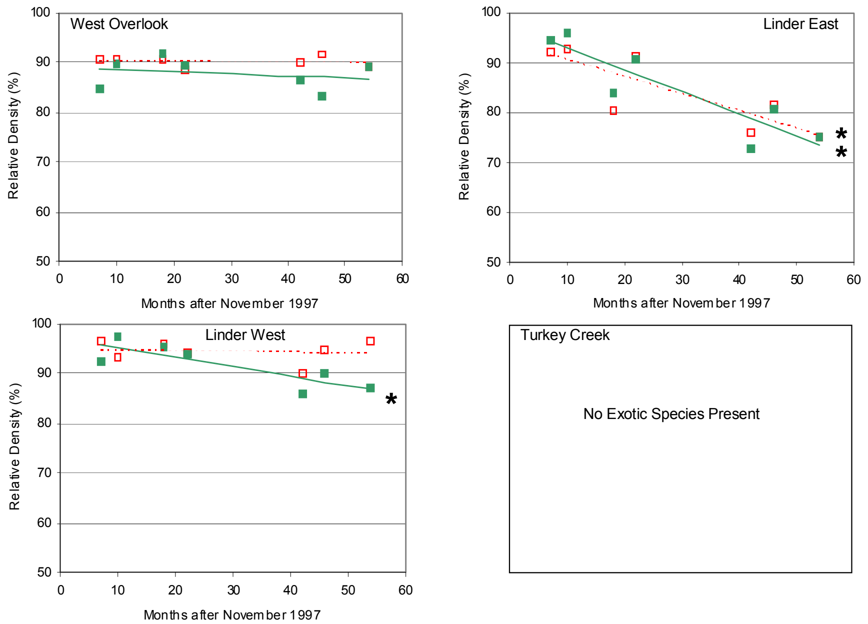

Fig. 7. Relative density of native woody seedling-sprout species at Coralville study sites from June 1998 to May 2002. Slopes and p-values for regression lines are given in Table 4. Significant linear regressions (p<0.10) are indicated with (*).

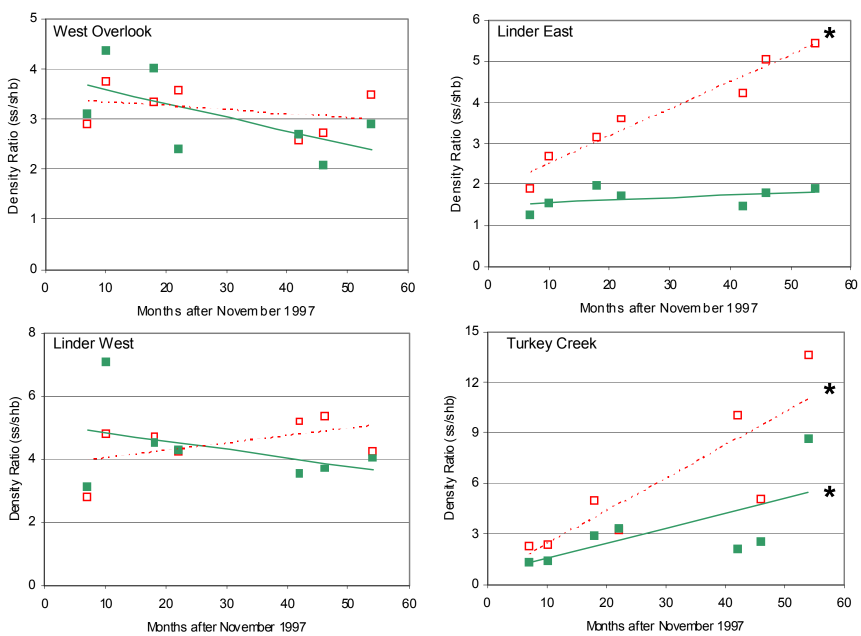

Fig. 8. Ratio of total seedling-sprout density to total shrub density at Coralville study sites from June 1998 to May 2002. Slopes and p-values for regression lines are given in Table 4. Significant linear regressions (p<0.10) are indicated with (*).

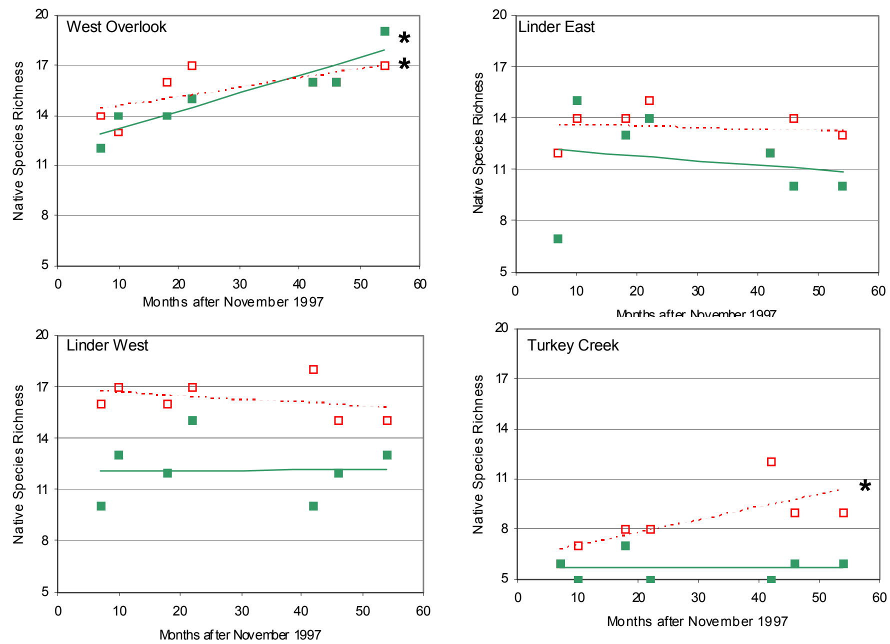

Fig. 9. Native species richness of seedling-sprouts at Coralville study sites from June 1998 to May 2002. Slopes and p-values for regression lines are given in Table 4. Significant linear regressions (p<0.10) are indicated with (*).

Table 5. Summary of local deer browse effects on seedling-sprouts at study sites West Overlook (WO), Linder East (LE), Linder West (LW), and Turkey Creek (TC). Arrows indicate either significant increase (↑) or decrease (↓) attributable to browsing. Assessment of that effect as either positive (pos) or negative (neg) to forest communities is presented.

Seedling-sprout Variable	WO	LE	LW	TC
Total Native Density	---	↑,pos	---	↓,neg
Total Exotic Density	↓,pos	---	↓,pos	---
Total All Density	---	↑,pos	↓,neg	↓,neg
Relative Native Density	---	---	↑,pos	---
Seedling-sprout/Shrub Index	---	↑,neg	---	↑,neg
Native Richness	↓,neg	---	---	↑,pos
Exotic Richness	---	↓,pos	---	---
Richness Quality Index	---	---	---	↑,pos

Shrubs

Shrubs were the woody size class that was most affected by browsing in this study. Six of the seven shrub variables exhibited uniform browse effects among all four sites (paired t-test p-values < 0.10, Table 6). Total native density of shrubs decreased due to browsing at all four sites, which contributed to an overall large-scale decrease in native shrub density due to browsing (Table 6, Fig. 10). At three sites, shrub density increased in the exclosure plot while the browse plots remained unchanged. At the fourth site, Turkey Creek, the shrub density in the exclosure remained unchanged while the browse plot decreased. In either scenario, the effective result is a decrease in shrub density due to browsing.

Browsing also significantly decreased the total density of exotic shrubs, but only at the Linder sites (Table 6, Fig. 11). At West Overlook exotic shrub density increased equally on both plots, and exotic shrubs were absent from Turkey Creek. The overall effect observed was a significant decrease in exotic shrub density due to browsing (Table 6).

Since the only significant changes in native and exotic shrub density were decreases, the browse effect on the total density of all woody shrub species was also a decrease. All four sites exhibited decreasing shrub density associated with browse plots, and together they contributed to an overall decrease in shrub density due to browsing (Table 6).

The relative density of native shrubs increased due to browsing on all three sites that had exotic shrubs present (Table 6, Fig. 12). Thus, although total densities of both native and exotic shrubs decreased more on browsed than unbrowsed plots, the decrease was relatively greater for exotic species.

Species richness of native shrubs was decreased by browsing on all four sites. These decreases were consistent enough to also produce an over all large-scale decrease in native shrub richness due to browsing (Table 6, Fig. 13). Exotic species richness of shrubs also decreased due to browsing on all three sites where exotic shrubs were present (all but Turkey Creek, Table 6, Fig. 14). However, a large amount of variation in this decrease prevented an overall browsing effect on exotic shrub richness. This was the only shrub variable that did not exhibit an overall uniform effect. The richness ratio index, which is a forest quality measure, decreased significantly on all four sites due to browsing and was significantly lower on browse plots overall (Table 6, Fig. 15). This means that although browsing caused decreases in both native and exotic shrub richness, the decrease was larger for native richness than exotic richness.

Table 6. Shrub density and species richness from 1998 to 2002 with linear regression and paired t-test results. Sites include West Overlook (WO), Lindner East (LE), Lindner West (LW), and Turkey Creek (TC). P-values less than 0.10 are considered slightly significant, those less than 0.05 are significant.

Variable	Site	Plot	Spring 1998	Fall 1998	Spring 1999	Fall 1999	Spring 2001	Fall 2001	Spring 2002	Reg Slope	P-value	Result Summary and Browse Effects
Total Native Density (st/m^2)	WO	Br	2.79	2.54	2.96	3.25	4.00	4.25	2.83	0.021	0.16	no change in browse, significant increase in exclosure; effective decrease indicated in browse
		Ex	2.21	2.04	2.58	4.13	4.08	4.54	3.54	0.042	0.044	
	LE	Br	2.00	1.54	1.79	1.96	2.08	1.92	1.92	0.0040	0.34	no change in browse, significant increase in exclosure; effective decrease indicated in browse
		Ex	2.71	2.67	3.17	3.17	3.54	3.83	3.13	0.017	0.056	
	LW	Br	3.38	2.83	2.92	3.79	3.25	2.79	3.75	0.0046	0.66	no change in browse, significant increase in exclosure; effective decrease indicated in browse
		Ex	2.33	1.33	2.38	2.50	3.42	2.88	2.96	0.027	0.040	
	TC	Br	1.46	1.29	0.83	0.96	0.50	0.63	0.38	-0.020	0.0015	significant decrease in browse, no change in exclosure; effective decrease indicated in browse
		Ex	1.38	1.33	0.83	0.88	1.21	1.00	0.79	-0.0067	0.24	
Mean 2002 Density and Regression Slope for all Browse Plots									2.22	-0.0051	0.017	overall - browse slope significantly lower than exclosure; significant decrease due to browse
Mean 2002 Density and Regression Slope for all Exclosure Plots									2.60	0.021		
Total Exotic Density (st/m^2)	WO	Br	0.63	0.83	0.71	0.96	1.17	1.58	1.54	0.019	0.0014	similar significant increase for both plots; no effect of browse indicated
		Ex	0.33	0.42	0.58	1.04	1.17	1.58	1.92	0.031	0.0004	
	LE	Br	0.54	0.58	0.38	0.58	0.17	0.29	0.13	-0.0093	0.0072	significant decrease in browse, no change in exclosure; effective decrease indicated in browse
		Ex	0.25	0.21	0.25	0.13	0.21	0.17	0.42	0.0018	0.42	
	LW	Br	0.00	0.00	0.08	0.08	0.08	0.08	0.13	0.0021	0.021	significant increase for both plots, browse increase smaller; effective decrease indicated in browse
		Ex	0.08	0.04	0.25	0.33	0.42	0.63	0.96	0.016	0.0016	
	TC	Br	0.00	0.00	0.00	0.00	0.00	0.00	0.00	no exotic spp.		no test in either plot
		Ex	0.00	0.00	0.00	0.00	0.00	0.00	0.00	no exotic spp.		
Mean 2002 Density and Slope for all Browse Plots									0.45	0.0041	0.014	overall - browse slope significantly lower than exclosure; significant decrease due to browse
Mean 2002 Density and Slope for all Exclosure Plots									0.82	0.016		
Total All Density (st/m^2)	WO	Br	3.42	3.38	3.67	4.21	5.17	5.83	4.38	0.040	0.028	significant increase for both plots, browse increase smaller; effective decrease indicated in browse
		Ex	2.54	2.46	3.17	5.17	5.25	6.13	5.46	0.073	0.0077	
	LE	Br	2.54	2.13	2.17	2.54	2.25	2.21	2.04	-0.0053	0.26	no change in browse, significant increase in exclosure; effective decrease indicated in browse
		Ex	2.96	2.88	3.42	3.29	3.75	4.00	3.54	0.018	0.016	
	LW	Br	3.38	2.83	3.00	3.88	3.33	2.88	3.88	0.0067	0.53	no change in browse, significant increase in exclosure; effective decrease indicated in browse
		Ex	2.42	1.38	2.63	2.83	3.83	3.50	3.92	0.043	0.0061	
	TC	Br	1.46	1.29	0.83	0.96	0.50	0.63	0.38	-0.020	0.0015	significant decrease in browse, no change in exclosure; effective decrease indicated in browse
		Ex	1.38	1.33	0.83	0.88	1.21	1.00	0.79	-0.0067	0.24	
Mean 2002 Density and Slope for all Browse Plots									2.67	0.0049	0.016	overall - browse slope significantly lower than exclosure; significant decrease due to browse
Mean 2002 Density and Slope for all Exclosure Plots									3.43	0.034		

Table 6

Variable	Site	Plot	Spring 1998	Fall 1998	Spring 1999	Fall 1999	Spring 2001	Fall 2001	Spring 2002	Reg Slope	P-value	Result Summary and Browse Effects
Native Relative Density (%)	WO	Br	81.7	75.3	80.7	77.2	77.4	72.9	64.8	-0.23	0.044	significant decrease for both plots, browse decrease smaller; effective increase indicated in browse
		Ex	86.9	83.1	81.6	79.8	77.8	74.1	64.9	-0.35	0.0032	
	LE	Br	78.7	72.5	82.7	77.0	92.6	86.8	93.9	0.38	0.0072	significant increase in browse, no change in exclosure; effective increase indicated in browse
		Ex	91.5	92.8	92.7	96.2	94.4	95.8	88.2	-0.016	0.81	
	LW	Br	100.0	100.0	97.2	97.8	97.5	97.1	96.8	-0.059	0.026	significant decrease for both plots, browse decrease smaller; effective increase indicated in browse
		Ex	96.6	97.0	90.5	88.2	89.1	82.1	75.5	-0.37	0.0040	
	TC	Br	100	100	100	100	100	100	100	no exotic spp.		no test in either plot
		Ex	100	100	100	100	100	100	100	no exotic spp.		
Mean 2002 Relative Density and Slope for all Browse Plots									88.85	0.030	0.075	overall - browse slope significantly higher than exclosure; slight significant increase due to browse
Mean 2002 Relative Density and Slope for all Exclosure Plots									82.16	-0.24		
Native Species Richness	WO	Br	8	8	6	8	5	6	4	-0.075	0.012	significant decrease in browse, no change in exclosure; effective decrease indicated in browse
		Ex	7	8	7	7	10	12	8	0.065	0.12	
	LE	Br	7	7	6	6	4	4	3	-0.085	0.000	significant decrease in browse, no change in exclosure; effective decrease indicated in browse
		Ex	8	9	10	12	10	11	11	0.044	0.15	
	LW	Br	6	7	6	7	3	3	3	-0.093	0.0047	significant decrease in browse, significant increase in exclosure; effective decrease indicated in browse
		Ex	5	6	8	6	8	9	8	0.063	0.030	
	TC	Br	5	5	4	3	1	2	2	-0.077	0.0045	significant decrease in browse, significant increase in exclosure; effective decrease indicated in browse
		Ex	3	4	3	4	4	4	5	0.027	0.056	
Mean 2002 Richness and Slope for all Browse Plots									3.00	-0.082	0.010	overall - browse slope significantly lower than exclosure; significant decrease due to browse
Mean 2002 Richness and Slope for all Exclosure Plots									8.00	0.023		
Exotic Species Richness	WO	Br	2	2	2	2	2	2	3	0.012	0.15	no change in browse, slight significant increase in exclosure; effective decrease indicated in browse
		Ex	3	4	5	6	6	6	5	0.041	0.10	
	LE	Br	2	1	1	1	1	1	1	-0.010	0.25	no change in browse, slight significant increase in exclosure; effective decrease indicated in browse
		Ex	1	1	1	1	2	1	2	0.019	0.071	
	LW	Br	0	0	1	1	2	1	2	0.038	0.012	significant increase for both plots, browse increase smaller; effective decrease indicated in browse
		Ex	1	1	1	2	2	3	3	0.045	0.0027	
	TC	Br	0	0	0	0	0	0	0	no exotic spp.		no test in either plot
		Ex	0	0	0	0	0	0	0	no exotic spp.		
Mean 2002 Richness and Slope for all Browse Plots									1.50	0.013	0.16	overall no significant difference in slopes for browse and exclosure plots; no browse effect
Mean 2002 Richness and Slope for all Exclosure Plots									2.50	0.035		

Table 6

Variable	Site	Plot	Spring 1998	Fall 1998	Spring 1999	Fall 1999	Spring 2001	Fall 2001	Spring 2002	Reg Slope	P-value	Result Summary and Browse Effects
Species	WO	Br	3.0	3.0	2.3	3.0	2.0	2.3	1.3	-0.030	0.013	significant decrease in browse, no change in exclosure; effective decrease indicated in browse
Richness		Ex	2.0	1.8	1.3	1.1	1.6	1.9	1.5	-0.0024	0.76	
Quality:	LE	Br	2.7	4.0	3.5	3.5	2.5	2.5	2.0	-0.029	0.049	significant decrease in browse, no change in exclosure; effective decrease indicated in browse
Native S		Ex	4.5	5.0	5.5	6.5	3.7	6.0	4.0	-0.014	0.58	
to	LW	Br	7.0	8.0	3.5	4.0	1.3	2.0	1.3	-0.13	0.0053	significant decrease in browse, no change in exclosure; effective decrease indicated in browse
Exotic S		Ex	3.0	3.5	4.5	2.3	3.0	2.5	2.3	-0.023	0.20	
Ratio	TC	Br	6	6	5	4	2	3	3	-0.077	0.0045	significant decrease for both plots, browse decrease larger; effective decrease indicated in browse
		Ex	4	5	4	5	5	5	6	0.027	0.056	
Mean 2002 Richness Index and Slope for all Browse Plots									1.90	-0.066	0.066	overall - browse slope significantly lower than exclosure; significant decrease due to browse
Mean 2002 Richness Index and Slope for all Exclosure Plots									3.44	0.0069		

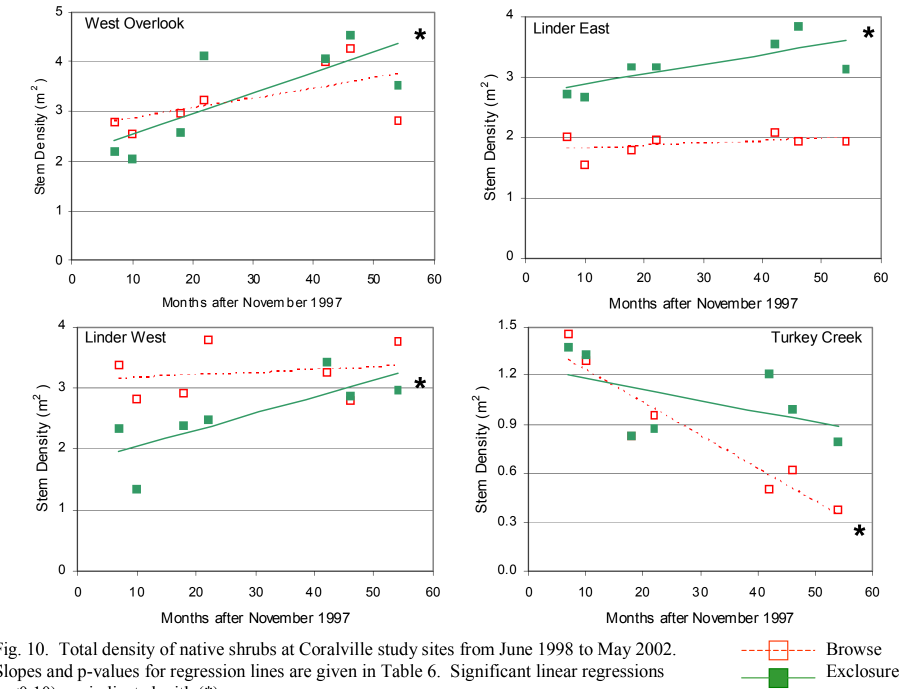

Fig. 10. Total density of native shrubs at Coralville study sites from June 1998 to May 2002. Slopes and p-values for regression lines are given in Table 6. Significant linear regressions (p<0.10) are indicated with (*).

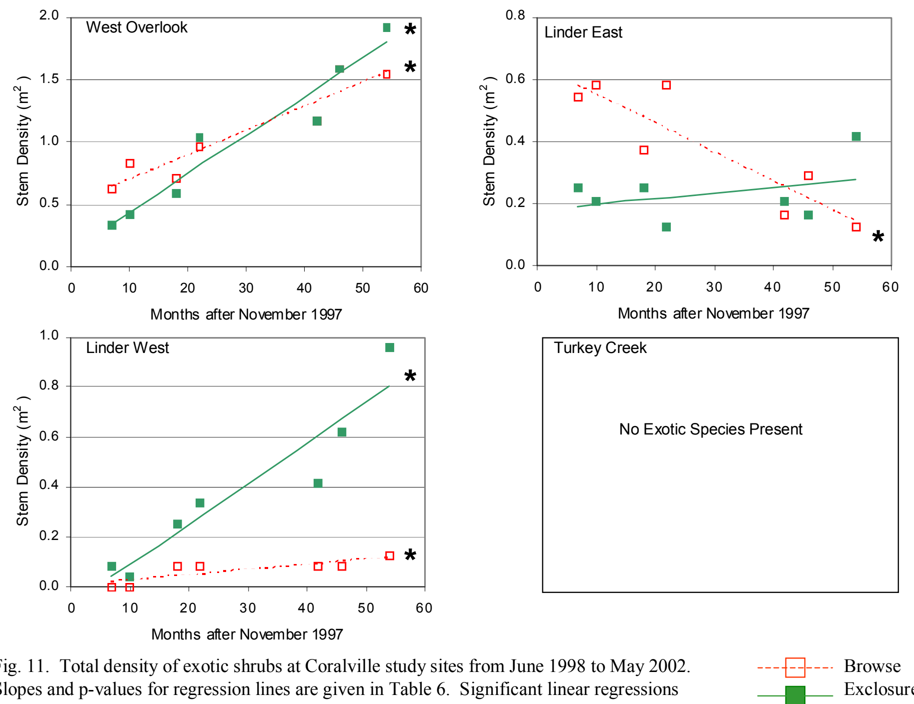

Fig. 11. Total density of exotic shrubs at Coralville study sites from June 1998 to May 2002. Slopes and p-values for regression lines are given in Table 6. Significant linear regressions (p<0.10) are indicated with (*).

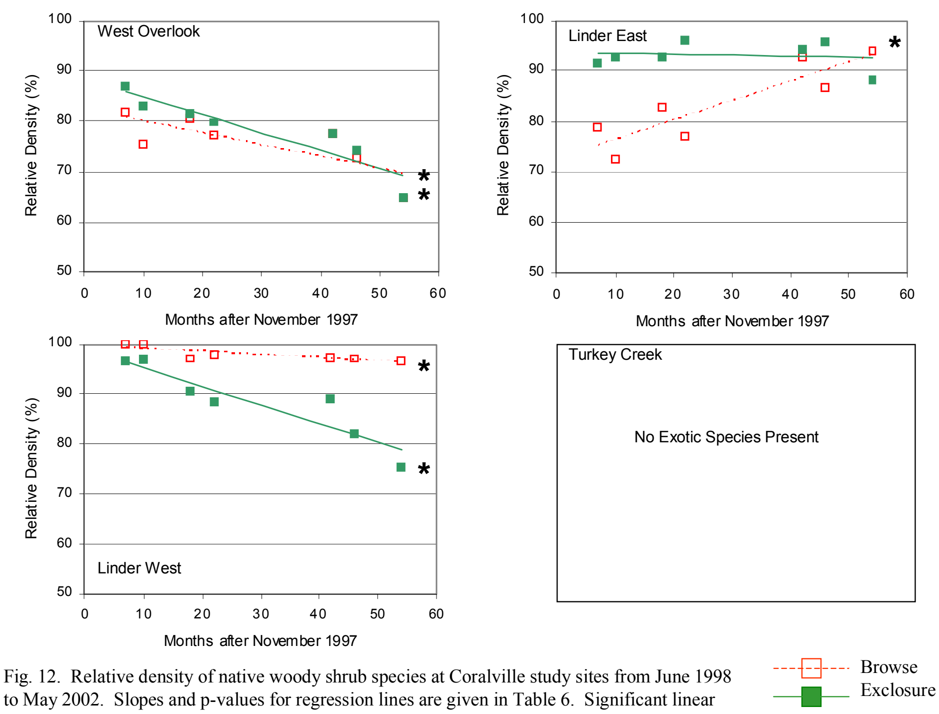

Fig. 12. Relative density of native woody shrub species at Coralville study sites from June 1998 to May 2002. Slopes and p-values for regression lines are given in Table 6. Significant linear regressions (p<0.10) are indicated with (*).

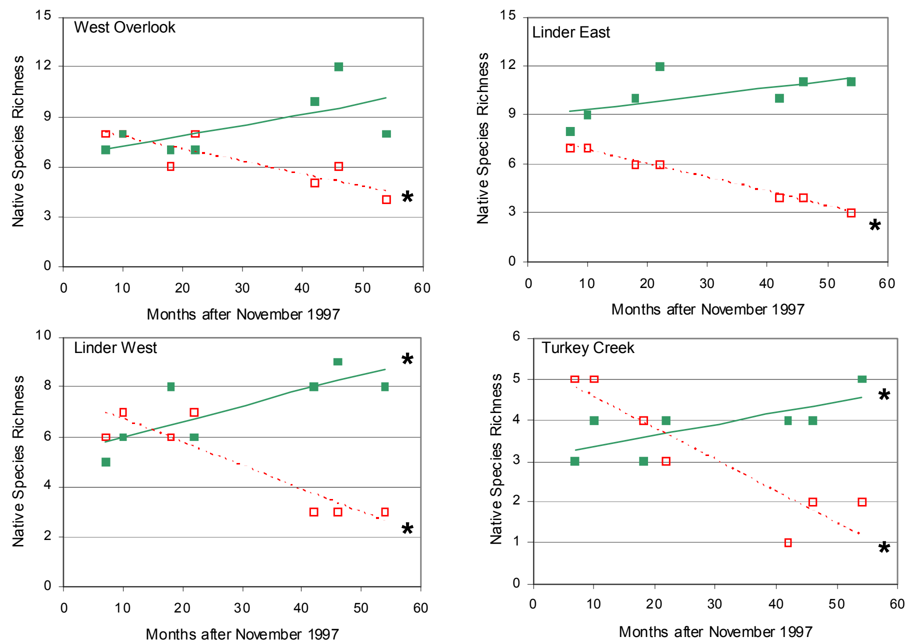

Fig. 13. Native species richness of shrubs at Coralville study sites from June 1998 to May 2002. Slopes and p-values for regression lines are given in Table 6. Significant linear regressions (p<0.10) are indicated with (*).

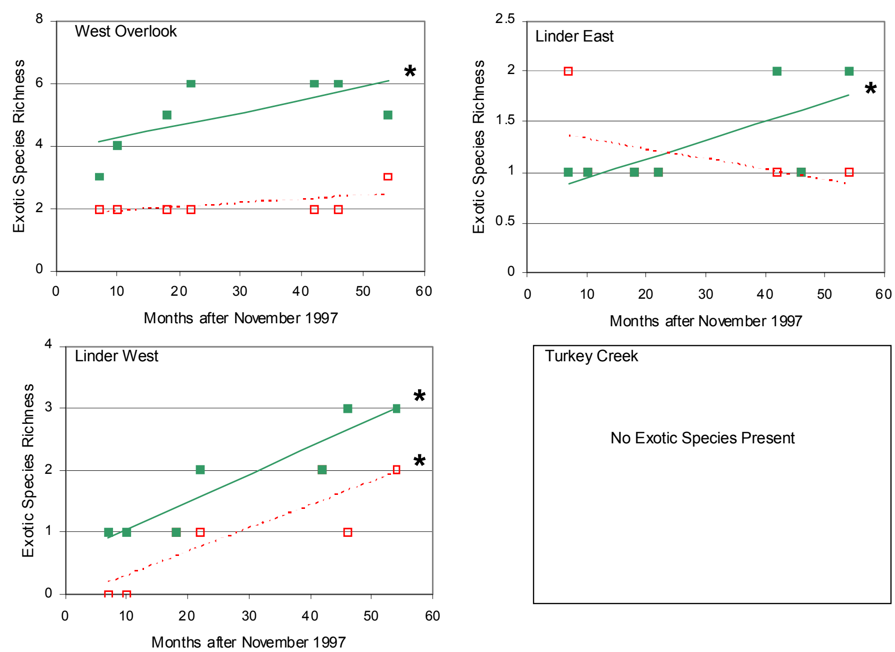

Fig. 14. Exotic species richness of shrubs at Coralville study sites from June 1998 to May 2002. Slopes and p-values for regression lines are given in Table 6. Significant linear regressions (p<0.10) are indicated with (*).

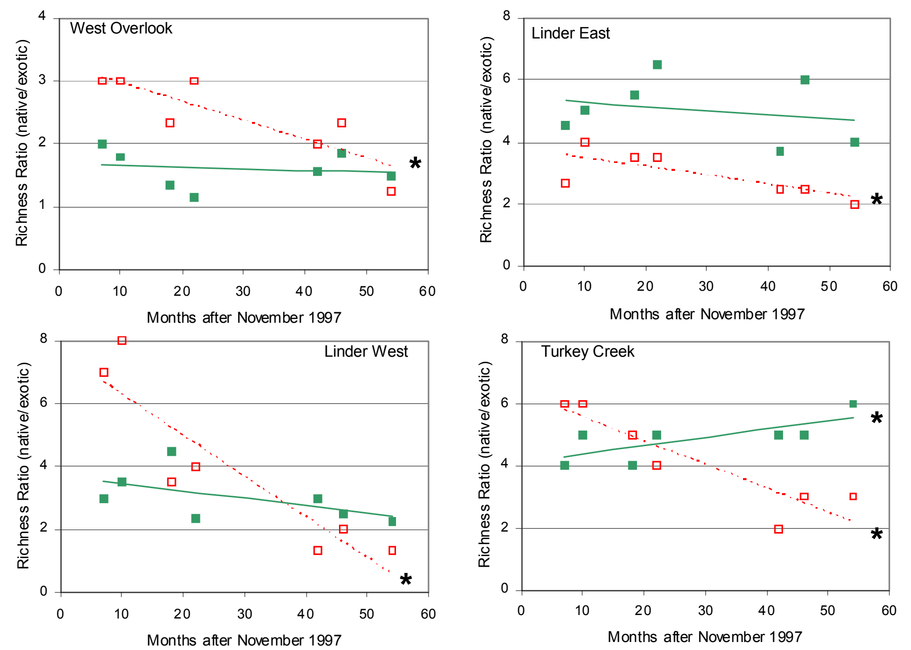

Fig. 15. Species richness quality ratio for shrubs at Coralville study sites from June 1998 to May 2002. Slopes and p-values for regression lines are given in Table 6. Significant linear regressions (p<0.10) are indicated with (*).

Compared to the seedling-sprouts, local shrub effects were much more common, significant and uniform. There were 24 local effects observed, of which 8 were positive (33%) and 16 were negative (67%) (Table 7). Thus it appears that browsing had a more negative influence on shrubs than on seedling-sprouts. All browsing effects on shrubs at Turkey Creek were negative, while 67% of there were negative at West Overlook and 57% were negative at the Linder sites (Table 7).

Table 7. Summary of local browse effects on shrubs at study sites West Overlook (WO), Linder East (LE), Linder West (LW), and Turkey Creek (TC). Arrows indicate either significant increase (↑) or decrease (↓) attributable to browsing. Assessment of that effect as either positive (pos) or negative (neg) to forest communities is presented.

Shrub Variable	WO	LE	LW	TC
Total Native Density	↓,neg	↓,neg	↓,neg	↓,neg
Total Exotic Density	---	↓,pos	↓,pos	---
Total All Density	↓,neg	↓,neg	↓,neg	↓,neg
Relative Native Density	↑,pos	↑,pos	↑,pos	---
Native Richness	↓,neg	↓,neg	↓,neg	↓,neg
Exotic Richness	↓,pos	↓,pos	↓,pos	---
Richness Quality Index	↓,neg	↓,neg	↓,neg	↓,neg

Saplings

Because of their larger size, saplings were expected to have fewer herbivory effects than either seedling-sprouts or shrubs. Although there were no significant browse effects on saplings demonstrated uniformly at all four sites (Table 8, paired t-tests all have $p>0.10$), there was at least one local site effect observed for every sapling variable except one. The total density of native saplings significantly decreased in both plots at Linder East, but the decrease was smaller in the browse plot, thus browsing resulted in an effective increase in the density of native saplings (Table 8, Fig. 16). No significant effect of browsing on the density of native saplings was observed at the other sites. The only effect of browsing on the total density of exotic saplings was an effective decrease observed at West Overlook (Table 8, Fig. 17). Total density of exotic saplings significantly increased in the exclosure plot, but remained unchanged in the browse plot. Total densities of all sapling species increased due to browsing at both of the Linder sites (Table 8).

The decrease in density of exotic saplings observed in the West Overlook browse plot seems to have contributed to an effective increase in the relative density of native saplings (Table 8, Fig. 18). This effect occurred when the relative density of native saplings decreased in the West Overlook exclosure but remained unchanged in the browse plot. No browse effects on the relative density of native saplings were recorded on the other sites.

Table 8. Sapling density and species richness from 1998 to 2002 with linear regression and paired t-test results. Data excluded *Celastrus*, *Parthenocissus*, and *Toxicodendron* lianas (see text). Sites include West Overlook (WO), Lindner East (LE), Lindner West (LW), and Turkey Creek (TC). P-values less than 0.10 are considered slightly significant, those less than 0.05 are significant.

Variable	Site	Plot	Spring 1998	Fall 1998	Spring 1999	Fall 1999	Spring 2001	Fall 2001	Spring 2002	Reg Slope	P-value	Result Summary and Browse Effects
Total	WO	Br	4125	4125	4225	3900	3275	3225	2775	-29.3	0.0004	similar significant decrease for both plots; no effect of browse indicated
Native		Ex	3800	3250	3575	3425	2600	2550	2250	-30.1	0.0012	
Density	LE	Br	1075	1050	925	975	700	725	675	-9.0	0.0001	significant decrease for both plots, browse decrease smaller; effective increase indicated in browse
(st/ha)		Ex	2300	2300	2450	2375	1550	1625	1550	-20.6	0.0038	
Fig.	LW	Br	1200	1025	1125	1025	850	850	750	-8.2	0.0014	similar significant decrease for both plots; no effect of browse indicated
		Ex	2000	1925	1850	2225	1575	1825	1550	-9.0	0.073	
	TC	Br	725	700	550	575	475	525	475	-4.8	0.0077	similar significant decrease for both plots; no effect of browse indicated
		Ex	675	675	600	700	500	500	475	-4.7	0.0036	
	Mean Slope for all Browse Plots									-12.8	0.33	overall no significant difference in slopes for browse and exclosure plots; no browse effect
	Mean Slope for all Exclosure Plots									-16.1		
Total	WO	Br	75	350	75	475	75	250	325	0.87	0.83	no change in browse, significant increase in exclosure; effective decrease indicated in browse
Exotic		Ex	100	100	100	100	175	250	250	3.57	0.0019	
Density	LE	Br	50	100	25	25	0	0	0	-1.59	0.026	similar significant decrease for both plots; no effect of browse indicated
(st/ha)		Ex	125	50	150	125	25	50	0	-2.27	0.061	
Fig.	LW	Br	0	0	0	0	0	0	0	no exotic spp.		no test in browse, no change in exclosure
		Ex	25	100	25	75	50	50	25	-0.44	0.53	
	TC	Br	0	0	0	0	0	0	0	no exotic spp.		no test in either plot
		Ex	0	0	0	0	0	0	0	no exotic spp.		
	Mean Slope for all Browse Plots									-0.80	0.62	overall no significant difference in slopes for browse and exclosure plots; no browse effect
	Mean Slope for all Exclosure Plots									0.65		
Total	WO	Br	4200	4475	4300	4375	3350	3475	3100	-28.5	0.002	similar significant decrease for both plots; no effect of browse indicated
All		Ex	3900	3350	3675	3525	2775	2800	2500	-26.5	0.002	
Density	LE	Br	1125	1150	950	1000	700	725	675	-10.6	0.0002	significant decrease for both plots, browse decrease smaller; effective increase indicated in browse
(st/ha)		Ex	2425	2350	2600	2500	1575	1675	1550	-22.9	0.005	
	LW	Br	1200	1025	1125	1025	850	850	750	-8.2	0.0014	significant decrease for both plots, browse decrease smaller; effective increase indicated in browse
		Ex	2025	2025	1875	2300	1625	1875	1575	-9.4	0.08	
	TC	Br	725	700	550	575	475	525	475	-4.8	0.0077	similar significant decrease for both plots; no effect of browse indicated
		Ex	675	675	600	700	500	500	475	-4.7	0.0036	
	Mean Slope for all Browse Plots									-13.01	0.44	overall no significant difference in slopes for browse and exclosure plots; no browse effect
	Mean Slope for all Exclosure Plots									-15.89		

Table 8

Variable	Site	Plot	Spring 1998	Fall 1998	Spring 1999	Fall 1999	Spring 2001	Fall 2001	Spring 2002	Reg Slope	P-value	Result Summary and Browse Effects
Native	WO	Br	98.2	92.2	98.3	89.1	97.8	92.8	89.5	-0.07	0.46	no change in browse, significant decrease for exclosure; effective increase indicated in browse
Relative		Ex	97.4	97.0	97.3	97.2	93.7	91.1	90.0	-0.16	0.001	
Density	LE	Br	95.6	91.3	97.4	97.5	100.0	100.0	100.0	0.14	0.02	similar significant increase for both plots; no effect of browse indicated
(%)		Ex	94.8	97.9	94.2	95.0	98.4	97.0	100.0	0.08	0.08	
Fig.	LW	Br	100.0	100.0	100.0	100.0	100.0	100.0	100.0	no exotic spp.		no test in browse, no change in exclosure
		Ex	98.8	95.1	98.7	96.7	96.9	97.3	98.4	0.01	0.74	
	TC	Br	100.0	100.0	100.0	100.0	100.0	100.0	100.0	no exotic spp.		no test in either plot
		Ex	100.0	100.0	100.0	100.0	100.0	100.0	100.0	no exotic spp.		
	Mean Slope for all Browse Plots									0.071	0.27	overall no significant difference in slopes for browse and exclosure plots; no browse effect
	Mean Slope for all Exclosure Plots									-0.041		
Native	WO	Br	8	6	8	6	7	7	8	0.009	0.69	no change in either, no effect of browse indicated
Species		Ex	7	7	8	9	9	8	8	0.022	0.24	
Richness	LE	Br	8	8	7	9	7	8	7	-0.017	0.36	no change in browse, slight decrease in exclosure; slight effective increase indicated in browse
		Ex	10	10	10	10	7	9	9	-0.040	0.098	
	LW	Br	9	9	9	9	7	8	8	-0.034	0.032	significant decrease in browse, no change in exclosure; effective decrease indicated in browse
		Ex	9	9	9	9	9	9	9	0	---	
	TC	Br	6	6	6	6	6	6	7	0.012	0.15	no change in browse, slight increase in exclosure; slight effective decrease indicated in browse
		Ex	4	4	5	5	5	5	5	0.019	0.063	
	Mean Slope for all Browse Plots									-0.008	0.86	overall no significant difference in slopes for browse and exclosure plots; no browse effect
	Mean Slope for all Exclosure Plots									-0.005		
Exotic	WO	Br	1	1	1	1	1	1	1	0	---	no change in either, no effect of browse indicated
Species		Ex	2	3	3	3	2	3	3	0.004	0.76	
Richness	LE	Br	1	2	1	1	0	0	0	-0.036	0.008	similar significant decrease for both plots; no effect of browse indicated
		Ex	2	1	2	2	1	1	0	-0.030	0.05	
	LW	Br	0	0	0	0	0	0	0	no exotic spp.		no test in browse, no change in exclosure
		Ex	1	1	1	1	1	1	1	0	---	
	TC	Br	0	0	0	0	0	0	0	no exotic spp.		no test in either plot
		Ex	0	0	0	0	0	0	0	no exotic spp.		
	Mean Slope for all Browse Plots									-0.018	0.50	overall no significant difference in slopes for browse

Mean Slope for all Exclosure Plots	-0.015	and exclosure plots; no browse effect

Table 8

Variable	Site	Plot	Spring 1998	Fall 1998	Spring 1999	Fall 1999	Spring 2001	Fall 2001	Spring 2002	Reg Slope	P-value	Result Summary and Browse Effects
Species	WO	Br	4.5	3.5	4.5	3.5	4.0	4.0	4.5	0.004	0.69	no change in either, no effect of browse indicated
Richness		Ex	2.7	2.0	2.3	2.5	3.3	2.3	2.3	0.004	0.70	
Quality:	LE	Br	4.5	3.0	4.0	5.0	8.0	9.0	8.0	0.117	0.002	significant increase for browse, no change for exclosure; effective increase indicated in browse
Native S		Ex	3.7	5.5	3.7	3.7	4.0	5.0	10.0	0.074	0.15	
to	LW	Br	10.0	10.0	10.0	10.0	8.0	9.0	9.0	-0.034	0.032	significant decrease for browse, no change for exclosure; effective decrease indicated in browse
Exotic S		Ex	5.0	5.0	5.0	5.0	5.0	5.0	5.0	0	---	
Ratio	TC	Br	7.0	7.0	7.0	7.0	7.0	7.0	8.0	0.012	0.15	no change in browse, slight increase in exclosure; slight effective decrease indicated in browse
Fig.		Ex	5.0	5.0	6.0	6.0	6.0	6.0	6.0	0.019	0.063	
	Mean Slope for all Browse Plots									0.021	0.67	overall no significant difference in slopes for browse and exclosure plots; no browse effect
	Mean Slope for all Exclosure Plots									0.0048		

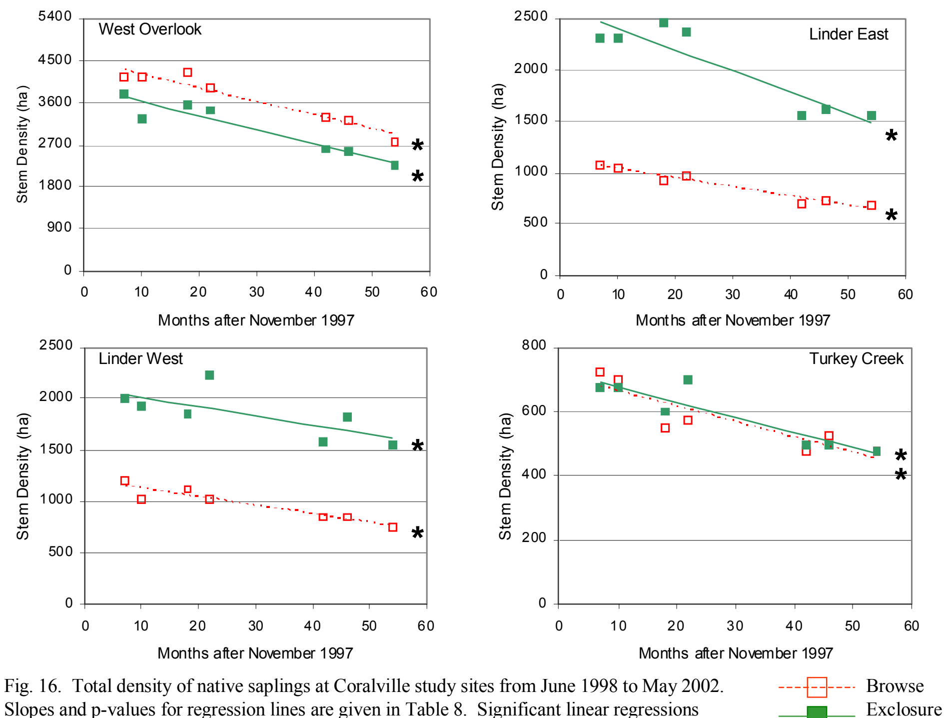

Fig. 16. Total density of native saplings at Coralville study sites from June 1998 to May 2002. Slopes and p-values for regression lines are given in Table 8. Significant linear regressions (p<0.10) are indicated with (*).

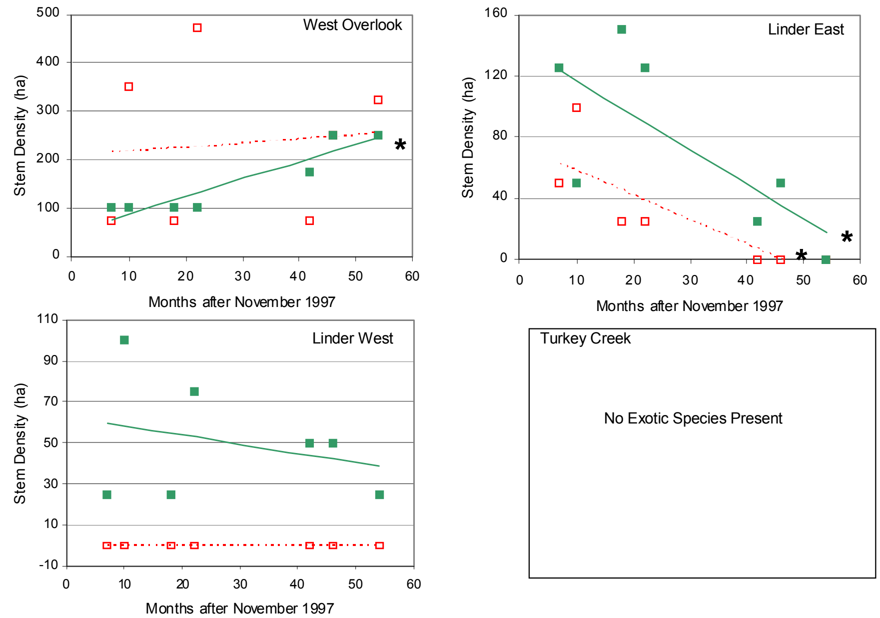

Fig. 17. Total density of exotic saplings at Coralville study sites from June 1998 to May 2002. Slopes and p-values for regression lines are given in Table 8. Significant linear regressions (p<0.10) are indicated with (*).

Browse
Exclosure

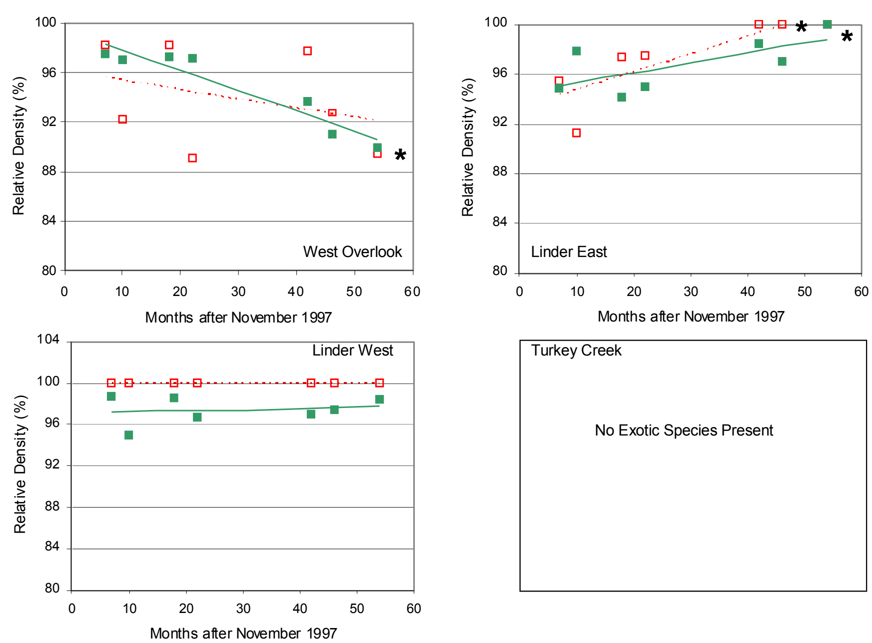

Fig. 18. Relative density of native woody sapling species at Coralville study sites from June 1998 to May 2002. Slopes and p-values for regression lines are given in Table 8. Significant linear regressions (p<0.10) are indicated with (*).

Browse
Exclosure

The native species richness of saplings increased due to browsing at Linder East, but decreased due to browsing at Linder West and Turkey Creek (Table 8). There were no measured effects of browsing on exotic species richness of saplings, thus the same pattern observed for native species richness was also observed for the species richness ratio. The ratio increased due to browsing on Linder East and decreased due to browsing on Linder West and Turkey Creek (Table 8, Fig. 19). The increase at Linder East occurred as the species richness ratio increased on the browse plot while the exclosure plot was unchanged. The decrease at Linder West occurred similarly, with a decrease in the richness ratio in the browse plot and no change in the exclosure. At Turkey Creek, an effective decrease occurred due to an increase in the richness ratio in the exclosure and no change in the browse plot (Table 8, Fig. 19).

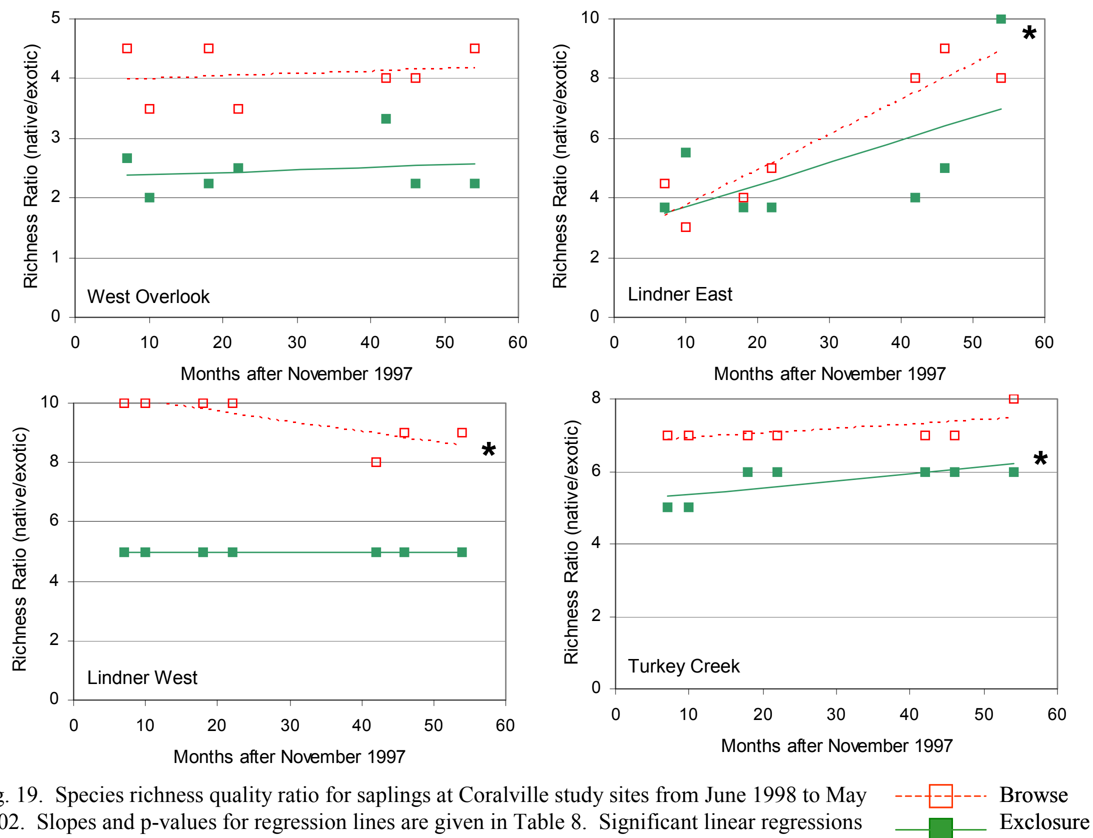

Fig. 19. Species richness quality ratio for saplings at Coralville study sites from June 1998 to May 2002. Slopes and p-values for regression lines are given in Table 8. Significant linear regressions (p<0.10) are indicated with (*).

Local effects of deer browsing on saplings were fewer than observed for seedling-sprouts and shrubs. There were 11 local effects observed, of which 7 were positive (64%) and 4 were negative (36%) (Table 9). Browse effects on saplings were positive at West Overlook and Linder East, and mostly negative at Linder West and Turkey Creek

Table 9. Summary of local browse effects on saplings at study sites West Overlook (WO), Linder East (LE), Linder West (LW), and Turkey Creek (TC). Arrows indicate either significant increase (↑) or decrease (↓) attributable to browsing. Assessment of that effect as either positive (pos) or negative (neg) to forest communities is presented.

Sapling Variable	WO	LE	LW	TC
Total Native Density	---	↑,pos	---	---
Total Exotic Density	↓,pos	---	---	---
Total All Density	---	↑,pos	↑,pos	---
Relative Native Density	↑,pos	---	---	---
Native Richness	---	↑,pos	↓,neg	↓,neg
Exotic Richness	---	---	---	---
Richness Quality Index	---	↑,pos	↓,neg	↓,neg

The variety of local site effects demonstrated among the four sites for seedling-sprouts, shrubs and saplings offers strong evidence for the view that deer herbivory effects depend enormously on many other factors in the environment. The one area of uniformity was the browse effects on shrubs. There is strong evidence that browsing reduces the density and richness of shrubs (native and exotic). Exotic density was more susceptible and decreased more than native density, which is good in that the relative density of native shrubs increases, but native density was still reduced. If a forest was overly dense with shrubs, then perhaps browsing could be described as a positive effect helping to open the understory and allow regeneration of canopy trees and growth of herbaceous species. That situation did not seem to be representative of the Coralville sites. By the end of the study in May of 2002, native density averaged 2.2 stems/m^2 in the browse plots and 2.6 stems/m^2 in the exclosure plots (Table 6), densities that do not seem to be overly dense for an upland forest. Native richness of shrubs was more susceptible to browsing than exotic richness, consequently the richness quality index decreased with browsing. Loss of native richness is always a negative outcome (assuming the excluded species were in their correct habitat). Mean native shrub richness in May 2002 was 3 in the browsed plots and 8 in the exclosure plots (Table 6). The native shrub species lost at Coralville included shagbark and bitternut hickory, hard maple, dogwood, blackberry, raspberry, wild grape and poison ivy, all of which are typical species of eastern upland deciduous forest. Their loss removes specific types of habitat structure and food production that could be important for other forest species. Loss of trees from the shrub layer, like hickory and maple, results in failed regeneration and contributes to the decline of those species in the forest canopy. It seems fairly safe to say that deer browsing effects on shrubs at Coralville have been detrimental to the forest community.

Because browse effects on seedling-sprouts and saplings was much more variable, it is more difficult to summarize those patterns. In general, positive effects slightly outnumbered negative effects for both of these size classes. It is possible that the negative effects of browsing on the shrub layer translate to positive effects on the seedling sprout layer. For example, decreasing shrub density and competition could favor increasing seedling-sprout density and richness, browsing effects which were observed at Linder East and Turkey Creek respectively.

At West Overlook, a relatively early successional forest with dense growth and high abundance of exotic species, browsing decreased the density of exotic seedling-sprouts and saplings. Given a high presence of exotic species to begin with, a decrease in exotic density due to browsing is consistent. Native richness of seedling-sprouts also decreased in the browse plots at West Overlook. Perhaps browsing combined with competition from dense seedling-sprout growth (May 2002 mean of 12 stems/m^2) was detrimental to some native seedling sprouts.

At Turkey Creek, the site most different from West Overlook due to its more mature forest community, absence of exotic species, and sparse growth of woody understory, browsing had many more effects especially on the seedling-sprout layer. Possibly because there was less vegetation to absorb the deer herbivory, browsing deceased native seedling-sprout density and increased the seedling-sprout/shrub density ratio, which suggests intense pressure on shrubs. If woody density is low to begin with, there is a good chance that herbivory will be more intense it terms of browsing pressure per stem. Although the density of native seedling-sprouts decreased due to browsing, native species richness and the richness quality index for seedling-sprouts increased. Apparently the low abundance of seedling-sprouts and shrubs combined with additional perturbance from browsing created ideal conditions for the establishment of new seedling-sprouts. Since exotic species are lacking from the vegetation at Turkey Creek, perhaps they are also absent from the seed bank and only native species were recruited. Sapling richness and richness quality index decreased due to browsing at Turkey Creek but was unaffected at West Overlook. Deer density in the tract containing Turkey Creek during 2000 and 2001 was the second highest among all the Coralville survey tracts. The combination of high deer numbers with low sapling abundance may be an important reason for the loss of a few low density sapling species, like red oak, from the browse plots

Browse Effects on Population Growth

The effect of deer browsing on specific species' population size and growth was assessed using per capita growth rates, in that way the repeated sampling technique was utilized in the analysis as a control for population size at the beginning of a survey period, or prior to the "treatment". Per capita growth rates (*r)* were compared between browse and exclosure plots with paired t-tests. Negative growth rates indicate the population decreased in size (lost individuals) over the specified time period, while positive growth rates signify the population increased in size (gained individuals).

Seedling-sprouts

There were nine taxa common enough over the sample dates and among the sites for inclusion in the analysis of browse effects (Table 10). Among these species, ten significant browse effects were identified ($p<0.10$), of which six were decreases in growth and four were increases in growth. Instances of native seedling-sprout species decreased by browsing included bitternut hickory during the 98-99 dormant season, oaks over the course of the whole study, and elms during both the 98-99 dormant season and the course of the whole study (Table 10). In the case of elm over the whole study period, populations in both the browse and exclosure plots increased in size, but the increase in the browse plot was significantly lower than in the exclosure plot, indicating a suppressing effect of browsing.

Instances of native seedling-sprout species increased by browsing were observed in black cherry, which increased during the summer 1998 and summer 1999 growing seasons, and in dogwood which increased significantly during the 98-99 dormant season (Table 10). During the summer 1999 season, black cherry seedling sprout populations decreased in size in both plots, but the decrease was significantly larger in the exclosure indicating an enhancement effect of browsing. Both black cherry and dogwood are successful edge/successional forest species, one of the habitat types favored by deer. Perhaps the increases these species demonstrated in this study result from adaptations they utilize to co-exist with deer.

The only exotic species analyzed was multiflora rose, and it exhibited mixed results. During the summer of 1998, browsing significantly increased its growth and density, but during the dormant season of 01-02, per capita growth on the browse plots was significantly lower than in the exclosure plots, although both plots exhibited positive growth rates (Table 10). Multiflora rose has numerous prickles and spines on its stems which probably provide some protection from herbivory during the summer when food is generally ample. Deer use of it may be limited to the dormant season when food is more scarce. Per capita growth rates calculated for multiflora rose over the entire study period were significantly lower on browse plots than the exclosure plots, thus there is evidence that deer herbivory might help control this exotic species.

Table 10. Population density and per capita growth (*r*) for common seedling-sprout species from June 1998 to May 2002. Paired t-test comparisons of mean per capita growth were completed between browse and exclosure plots on each pair of sequential sample dates and for the entire study period. Boldface means are significantly different at p<0.10.

			June 1998	Sept 1998	May 1999	Sept 1999	May 2001	Sept 2001	May 2002	June 98 to May 02
Bitternut hickory	mean stem density (m^2)	Browse	0.16	0.18	0.15	0.25	0.14	0.29	0.18	
		Exclosure	0.15	0.08	0.17	0.21	0.14	0.14	0.14	
	mean per capita growth	Browse	-1.25	**-0.31**	1.68	-0.10	2.59	-0.93		0.030
		Exclosure	-1.10	**1.36**	-0.84	-0.12	1.07	-0.56		0.035
Black cherry	mean stem density (m^2)	Browse	1.34	1.53	1.92	1.33	1.48	1.52	1.66	
		Exclosure	1.01	0.74	1.07	0.60	0.78	0.58	1.28	
	mean per capita growth	Browse	**0.18**	0.73	**-1.57**	0.27	-2.06	1.23		0.148
		Exclosure	**-1.97**	0.44	**-2.51**	0.34	-1.86	2.17		0.094
Oak sp.	mean stem density (m^2)	Browse	0.10	0.13	0.07	0.06	0.06	0.06	0.02	
		Exclosure	0.03	0.05	0.01	0.02	0.04	0.08	0.04	
	mean per capita growth	Browse	-1.19	-0.61	-0.95	0.0	-0.28	-0.93		**-0.444**
		Exclosure	0.96	-1.20	0.44	0.30	2.15	-0.60		**0.105**
Gooseberry sp.	mean stem density (m^2)	Browse	0.90	0.78	1.26	1.02	1.42	1.02	1.54	
		Exclosure	0.64	0.66	1.10	0.94	1.17	0.93	1.38	
	mean per capita growth	Browse	-0.50	1.33	-0.54	0.29	-1.22	0.86		0.315
		Exclosure	2.25	0.98	-1.11	0.19	-1.35	1.05		0.364
Bittersweet sp.	mean stem density (m^2)	Browse	3.53	4.21	4.29	5.85	6.24	6.64	6.90	
		Exclosure	2.65	3.22	3.75	4.26	4.26	4.69	5.67	
	mean per capita growth	Browse	0.46	0.02	1.10	0.04	0.25	0.04		0.169
		Exclosure	0.75	0.21	0.18	-0.06	0.93	0.13		0.176
Dogwood sp.	mean stem density (m^2)	Browse	0.07	0.11	0.19	0.23	0.16	0.10	0.09	
		Exclosure	0.10	0.26	0.22	0.28	0.19	0.16	0.20	
	mean per capita growth	Browse	1.12	**1.14**	0.37	-0.12	-1.64	-0.54		0.016
		Exclosure	3.08	**-0.19**	0.68	-0.06	-0.92	0.26		0.162

Table 10			June 1998	Sept 1998	May 1999	Sept 1999	May 2001	Sept 2001	May 2002	June 98 to May 02
Blackberry Raspberry	mean stem density (m^2)	Browse	0.11	0.22	0.19	0.21	0.24	0.29	0.25	
		Exclosure	0.03	0.14	0.14	0.08	0.21	0.22	0.19	
	mean per capita growth	Browse	1.85	0.55	0.21	0.02	0.51	0.23		0.319
		Exclosure	5.03	0.00	-0.80	0.10	-1.51	2.25		0.552
Elm sp.	mean stem density (m^2)	Browse	0.35	0.51	0.29	0.71	0.36	0.47	0.43	
		Exclosure	0.31	0.43	0.60	0.73	0.34	0.51	0.96	
	mean per capita growth	Browse	3.52	**-0.62**	1.51	-0.82	2.18	0.96		**0.247**
		Exclosure	-0.88	**0.29**	1.46	-0.50	0.66	2.44		**0.378**
Multiflora rose	mean stem density (m^2)	Browse	0.25	0.28	0.67	0.42	1.29	0.86	1.22	
		Exclosure	0.15	0.10	0.51	0.24	1.01	0.57	1.07	
	mean per capita growth	Browse	**0.66**	0.86	-0.93	0.72	-2.02	**0.50**		**0.331**
		Exclosure	**-1.80**	2.28	-1.83	0.84	-1.53	**0.94**		**0.505**

Oak seedling-sprouts were the only taxa analyzed that exhibited a seasonal effect of browsing. Per capita growth rates on browse plots were about 2 stems/stem lower than growth rates in exclosure plots during the summer; while per capita growth rates on browse plots during the dormant season were about 0.1 stem/stem higher than exclosure plots ($p=0.028$, two sample t-test). These results suggest that oak seedling-sprout stems are more susceptible to deer herbivory and likely to suffer mortality during the summer than during winter.

The loss of oak and bitternut hickory seedling-sprouts from deer herbivory is an important concern for forest managers, as these species, especially oak, are key canopy species. Oak shrubs and saplings were very uncommon in the study; shrubs were only observed in the Turkey Creek exclosure, and saplings were only observed in the West Overlook browse and Turkey Creek exclosure.

Three taxa in the analysis appeared to be oblivious to deer browsing. No browse effects of any type were observed for seedling-sprouts of gooseberry, bittersweet, and blackberry/raspberry.

Shrubs

Six of the nine seedling-sprout species analyzed were common enough as shrubs to be included in the analysis of browse effects on shrub populations. Browse effects were observed for all six taxa, including the three species that were unaffected as seedling-sprouts. There were nine instances of browse effects among these six species. Shrubs are clearly more likely to be affected by deer herbivory than are seedling-sprouts. Like the seedling-sprouts, the type of browse effect on shrubs was split nearly 50%, with five instances of decreasing population growth and four instances of increasing population growth. Whereas in the seedling-sprouts, only 11% of the species exhibited mixed results depending on time, in the shrubs 33% of the species exhibited mixed results. It seems that season plays a more important part in determining the browse effects in shrubs.

The per capita growth rate of black cherry shrubs decreased in the browse plots during the 98-99 dormant season (Table 11). This is an opposite effect as observed in the seedling-sprouts where browsing increased growth, at least during the growing season. Since the effects occurred at different times of the year, it may be that black cherry does fine during the summer but is susceptible to browsing during the winter (especially the taller shrubs).

Another species that was more adversely affected as a shrub than a seedling-sprout is dogwood. Its per capita growth rate on browse plots was significantly lower than on exclosure plots during the 20-month period from September 1999 to May 2001.

Bittersweet and multiflora rose both displayed an instance of increased population growth due to browsing. The per capita growth of bittersweet shrubs on the browse plots was significantly higher than in exclosure plots during the 01-02 dormant season (Table 11). The same pattern occurred in multiflora rose during the 1998 growing season. In both of these instances, most of the difference in per capita growth was due to very low growth rates in the exclosures.

Gooseberry shrubs exhibited a pattern very similar to the multiflora seedling-sprouts. Browsing produced an increase in population growth during the summer season of 1999 and a decrease in population growth during the 20-month period from September 1999 to May 2001. An over all effect (over the entire study period) was observed for gooseberry as a decrease in per capita growth due to browsing (Table 11).

Lastly, blackberry/raspberry shrubs increased in population size due to browsing during the 1998 summer season, and then exhibited a significantly lower per capita growth rate on the browse plot compared to the exclosure plot during the 20-month period from September 1999 to May 2001 (Table 11).

Gooseberry was the only taxa that exhibited an effect of season on browse effects. Per capita growth rates on browse plots were about 0.4 stems/stem higher than growth rates in exclosure plots during the summer; while per capita growth rates on browse plots during the dormant season were about 0.25 stems/stem lower than exclosure plots ($p=0.059$, two sample t-test). In other words, summer browsing was favorable to gooseberry, but winter browsing was detrimental. Being a species with a prickly stem, gooseberry may be favored by selective herbivory to avoid it in the summer when food is fairly plentiful, but susceptible to browsing in the winter when food is scarce.

Table 11. Population density and per capita growth (*r*) for common shrub species from June 1998 to May 2002. Paired t-test comparisons of mean per capita growth were completed between browse and exclosure plots on each pair of sequential sample dates and for the entire study period. Boldface means are significantly different at p<0.10.

			June 1998	Sept 1998	May 1999	Sept 1999	May 2001	Sept 2001	May 2002	June 98 to May 02
Black cherry	mean stem density (m^2)	Browse	0.13	0.11	0.07	0.08	0.11	0.07	0.04	
		Exclosure	0.34	0.24	0.41	0.36	0.38	0.31	0.40	
	mean per capita growth	Browse	-0.59	**-0.76**	0.44	0.13	-0.65	-0.38		-0.195
		Exclosure	-0.09	**0.20**	0.19	-0.07	-0.28	0.19		0.023
Gooseberry	mean stem density (m^2)	Browse	0.63	0.49	0.44	0.50	0.32	0.32	0.32	
		Exclosure	0.68	0.59	0.59	0.63	0.90	0.86	0.76	
	mean per capita growth	Browse	-0.88	-0.06	**0.33**	**-0.18**	-0.07	-0.008		**-0.122**
		Exclosure	-1.57	0.43	**0.03**	**0.61**	-0.41	0.02		**0.203**
Bittersweet	mean stem density (m^2)	Browse	1.71	1.35	1.71	2.03	2.54	2.44	2.40	
		Exclosure	0.93	0.67	0.99	1.28	1.47	1.42	1.06	
	mean per capita growth	Browse	-1.01	0.32	0.64	0.12	-0.15	**0.02**		0.0867
		Exclosure	-1.32	0.55	0.41	0.09	-0.38	**-0.30**		-0.004
Dogwood	mean stem density (m^2)	Browse	0.06	0.08	0.06	0.09	0.00	0.02	0.01	
		Exclosure	0.11	0.19	0.20	0.33	0.23	0.28	0.14	
	mean per capita growth	Browse	1.91	-0.32	0.92	**-1.31**	1.68	-0.22		-0.309
		Exclosure	1.41	-0.11	1.24	**-0.11**	0.44	-0.87		0.021
Blackberry Raspberry	mean stem density (m^2)	Browse	0.18	0.22	0.15	0.19	0.04	0.08	0.03	
		Exclosure	0.15	0.11	0.14	0.19	0.17	0.24	0.18	
	mean per capita growth	Browse	**0.60**	-0.47	0.07	**-1.02**	0.66	-0.51		-0.502
		Exclosure	**-1.78**	0.59	0.54	**0.00**	0.53	-1.34		-0.153
Multiflora rose	mean stem density (m^2)	Browse	0.18	0.21	0.17	0.25	0.11	0.15	0.14	
		Exclosure	0.18	0.14	0.25	0.21	0.33	0.33	0.65	
	mean per capita growth	Browse	**0.20**	0.90	1.02	-0.29	-0.84	0.61		0.164
		Exclosure	**-1.30**	1.09	-0.66	0.22	0.0	1.01		0.312

Literature Review

Numerous studies have been undertaken to study the role of deer herbivory in the ecology of forests. A few of those studies are reviewed here to provide additional insight into the effects deer on forest vegetation. Strole and Anderson (1992) studied the species preferences deer have for browsing by measuring twigs in ten upland forests in central Illinois. A total of 35 woody species were browsed by deer; 22 of those were common enough to be included in the analysis. The overall browse rate was 14% (browsed twigs out of total twigs). Species with the highest relative use (% twigs browsed among all browsed twigs) were black cherry (42%), multiflora rose (9%), sugar or hard maple (5%), black haw (5%) and white oak (5%). Amount of use by deer depends in part on the amount of browse available. Use of maple and to some extent black cherry was high because these species comprised a large amount of the species abundance in the forests. Nine species were browsed in significantly greater proportion than available (i.e., preferred species). These included choke cherry, gray dogwood, multiflora rose, white oak, shagbark hickory, hackberry, basswood, black haw, and black cherry (Strole and Anderson 1992). Six species were low preference or used less than availability would predict. These included hazel, gooseberry, prickly ash, sugar (hard) maple, red haw and white ash. The remaining seven species were used in an amount proportional to their abundance: American elm, red elm, ironwood, Ohio buckeye, bitternut hickory, green briar, and box elder. In general, this study showed that deer took a disproportionately large amount of browse from relatively uncommon species. Changes to forest species composition could occur through reduction in preferred species and favoring browsing tolerant and low preference species. The observation that shade tolerant sugar (hard) maple and white ash were significantly non-preferred by deer as browse while white oak was the fourth most preferred species, casts serious concern on the already low regeneration of oak in upland oak forests and their replacement by shade tolerant species such as maple and ash, a pattern thought to be exacerbated by fire exclusion.

Fletcher et al. (2001) studied the effects of deer herbivory on several forest herbaceous species using exclosures in Virginia. For all five species studied (bellwort, false Solomon's seal, Solomon's seal, showy orchid, and jack-in-the-pulpit) reproductive activity measured as frequency of flowering or fruiting plants was significantly reduced by deer herbivory (typically by 70% to 100%). The size of individual plants was also affected by deer herbivory. For all species except showy orchid (which has basal leaves and a low profile), plants inside exclosures were larger than plants outside. This difference likely contributed to the reproductive differences observed. Deer selectively graze taller plants effectively reducing their photosynthetic capability, which may lower energy availability for producing flowers and fruits (Fletcher et al. 2001). A negative effect of herbivory on the density of plants was also observed for three of the species. Density of bellwort, false Solomon's seal, and Solomon's seal was significantly lower outside exclosures than inside. The authors suggest that monitoring reproductive activity of lily and orchid species can serve as a rapid assessment method for measuring the severity of deer grazing on herbaceous species.

In an Indiana study with similar goals of rapid assessment of deer grazing (Webster and Clark 2000, Webster et al. 2001), it was demonstrated that monitoring the plant height of sweet cicely, jack-in-the-pulpit, and white baneberry can provide managers with a simple and accurate method of assessing the impact of deer herbivory on forest plant communities. The authors felt that after recalibration, the basic relationship they found between the heights of these species and grazing intensity would apply to other similar forest communities in the lower Midwest.

Deer herbivory in northern Wisconsin forests was studied by measuring forest community structure and composition at 12 sites and comparing vegetation variables with measurements of deer density (Balgooyen and Waller 1995). Frequency of mountain maple, yellow birch, mountain-ash, and Canada yew all declined in response to increasing deer density. One herbaceous species, bluebead lily, also decreased in frequency and cover in response to increasing deer density. Other herbaceous species observed to be grazed and damaged by deer included large-leaved aster, wild sarsaparilla, bloodroot, false Solomon's seal, twisted rosy stalk, nodding trillium, white trillium and bellwort. Canada mayflower exhibited a positive response, increasing in frequency, to deer density. This study also demonstrated that deer herbivory can have long-term consequences. For some species, high historic deer density was associated with decreased abundance, for example the frequency of

Canada yew, the frequency of Canada mayflower and bluebead lily, and the cover of wild sarsaparilla, Canada mayflower and bluebead lily (Balgooyen and Waller 1995).

The only other research on deer herbivory known to have been done in Iowa is one conducted in central Iowa (Rosburg 2002). This study monitored forest community composition and structure in plots located inside and outside exclosures at three study sites over a three year period. Although there were no significant differences in herbaceous structure and diversity between grazed and exclosure plots, there were some tendencies noted. Greater herbaceous growth (total stem density and frequency) was apparent in exclosures after three years of deer exclusion. Native herbaceous diversity also tended to be higher in exclosures, apparently due to the release from grazing exerting a tendency to increase evenness.

Deer herbivory was shown to decrease native shrub density. Shrub density in the exclosure plots was over twice as high as in the browsed plots (Rosburg 2002). One beneficial aspect of deer herbivory was that the evenness of native seedling-sprouts was increased by browsing. Perhaps the more open environment presumably created by the browsing of shrubs improved the environment for seedling-sprout growth.

A few specific effects of herbivory on species density were demonstrated. The density of green briar seedling-sprouts was 2.5 times greater in exclosures than in browsed plots. Also an increase in the density of sedges in the exclosure compared to grazed plots was observed. Although lacking significance, several species exhibited population growth rates that tended to be higher in the exclosure than in the grazed plots, including oak and elm seedling-sprouts, bedstraw, violets, and enchanter nightshade. Two species, black snakeroot and hickory seedling-sprouts, tended to have higher growth rates in the grazed plots over the three year study and therefore seemed to be favored by deer herbivory (Rosburg 2002).

A few other notable effects on species frequency were observed at the individual study sites (not uniformly observed at all sites). Some additional species that exhibited significant decreases in frequency due to deer herbivory in a local environment were: kidney leaf buttercup, white avens, cleavers bedstraw, woodland tick-trefoil, spring beauty, and white trout lily. Only a few species demonstrated an increase from herbivory in a local environment; these included woodland fescue, sweet-scented bedstraw, and white trout lily (Rosburg 2002).

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